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Molluscan Research

Molluscan Research is a publication for authoritative scientific papers dealing with the Phylum Mollusca and related topics. Two numbers are published in each annual volume. General and theoretical papers relating to molluscs are welcome. Papers concerning specific geographical areas or new taxa should normally focus on the Indo-West Pacific region, as well as Australasia and the Southern Ocean.

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- All pages of the manuscript must be numbered consecutively, including those carrying references, tables and figure captions, all of which are to be placed after the text.
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- **Original artwork must not be submitted prior to the final acceptance of the manuscript.** Artwork will be returned, if this is requested at the time of acceptance.
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- The **abstract** should be fewer than 200 words and should state concisely the scope of the work and give the principal findings. It should be complete enough for direct use by abstracting services.
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- **Headings** for Introduction, Materials and methods, Results, Discussion, Acknowledgments and References should be in bold (in 12 pt) and on the left margin.

Taxonomic papers

- Headings for all taxonomic categories in taxonomic papers should be centred.
- Under each species or group taxon heading, list the headings in the following order: [Synonymy]; Type material; Other material examined; Diagnosis (optional); Description; Distribution; Remarks; Etymology.
- Authors' names and dates should be used for genus-group and species-group names used in headings. The abbreviations 'n. gen.', 'n. sp.', or 'n. subsp.' should be used for indicating a new genus, species, or subspecies.
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Examples of format for species synonymy:

Xus yus Smith, 1902: 304, pl. 3, fig. 4A (Type locality: Big Bay, Sydney, Australia. Holotype, Museum acronym, registered number; 4 paratypes, Museum acronym, registered number); Jones, 1934: 456; Dick, 1956: 23, pl. 2, fig. 6. [Example of an available name.]

Wus yus (Smith, 1902). Gail, 1978: 56, pl. 4, fig. 5. [Example where genus name has been changed.]

Xus mus. – Hope, 1987: 21, pl. 3, fig. 8; Fred, 2000: 400 (not of Black, 1934). [Example of misidentification.]

Example of format for genus synonymy:

Xus Smith, 1902: 303. Type species (by subsequent designation of Jones, 1934: 456): *Xus yus* Smith, 1902; Recent, Bolivia.

Wus Gail, 1978: 56. Type species (original designation): *Xus yus* Smith, 1902; Recent, Bolivia.

- Type details may be added in the format shown above.
- Multiple synonyms should be arranged in order of date of first application to the unit in question, and under each name the separate references (if more than one is given) should be in chronological order.
- If synonymies and references have previously been published these should not be repeated in full, if a reference to that source is given.
- The type species, with author and date, should be cited immediately beneath the synonymy for each genus treated.
- **Type details** should be given for each valid species treated, the museum in which the primary type (holotype, syntypes, lectotype or neotype) is preserved should be given or, if the whereabouts of the type are unknown, what steps were taken to ascertain its whereabouts.
- All types of new taxa must be lodged in a public museum. Authors should make every effort to ensure that types are lodged in the most appropriate institution in the region from which the species originates and in accordance with the requirements of collecting permits or legislation.
 - Authors should be aware of the Australian Wildlife Protection (Regulation of Exports and Imports) Act 1982 and associated Regulations 1984, which govern the import and export of all specimens of Australian wildlife. Among other things the Act requires that any specimen exported from Australia after 1 May 1984 and that is subsequently designated a primary type of an Australian native animal must be lodged in an Australian institution. Further details may be obtained from the Director, Environment Australia, GPO Box 636, Canberra, ACT 2601, Australia.
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 - Information for **type material** should include a summary of all available locality, habitat and collection data. It should follow the same format as given for non-type material.
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 Locality, lat. long., etc.
 - Collection date should be given in the form 2 Aug. 2001.
 - For large material examined sections, authors should minimise the information to locality, repository, registered number and number of specimens only, and should summarise the information from label data in distribution maps or in the main text. Use bold headings for country and state names, etc.
 - Records should normally be arranged geographically from north to south and east to west where practical.
 - Museum acronyms should conform to those normally used. They should be spelt out in a list under Materials and methods. Museum registered numbers should be cited in the form C.3000 or F4000 not C 3000 or F 4000. Citation of numbers of specimens should follow the registered number in the form C.3000 (2). You may wish to specify details such as separate valves, empty shells, etc.; this can be done using abbreviations, e.g. C.3000 (2v, 1c).
 - **Avoid needless repetition:** group common localities together in the following way:
 Sydney Harbour: Balmoral Beach, Lat. Long., date, museum, registered number (number of specimens); Vaucluse, Lat. Long., date, museum, registered number (number of specimens).
 Botany Bay: etc.
 Multiple lots from the same locality should be given in the following way:
 Balmoral Beach, Lat. Long.: date, museum, registered number (number of specimens); date, museum, registered number (number of specimens). Botany Bay, etc.
 - Summarise distributions in a **distribution map**.
 - Information regarding distribution, habitat, host association, seasonality, behaviour, or biology should be summarised in the body of the paper.
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 - The 'telegraphic' style is required for both.
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 - Descriptions should be subdivided by appropriate subordinate headings in italics at the left margin.
 - Comparative comments are to be placed under 'Remarks'.
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- **Measurements.** Descriptions should be enhanced by the presentation of precise measurements of the type material and other relevant material in table format. All tables must be numbered (see Tables below). For shelled species, measurements of more than just length and width are encouraged.

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- **Statistical tests** should be described briefly and, if necessary, supported by references. Numbers of individuals, mean values, ranges and measures of variability should be stated. It should be made clear whether the standard deviation or the standard error of the mean has been given.
- The **International Code of Zoological Nomenclature** (Fourth Edition, effective from 1 January 2000) and decisions by the ICZN must be adhered to.
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- **Footnotes.** Footnotes in the text are discouraged and should be used only when essential. They should be placed within horizontal rules immediately under the lines to which they refer.
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 - When citing distances and measurements insert a single space between the number and the dimension (e.g. 5 mm, not 5mm).

References

References should be cited in the text with the year of publication, e.g. Shepherd and Cannon (1988) or (Shepherd and Cannon 1988; Smith 1992, 1995). Note that commas are not used between the name and date in cited references. However, for authors of names, a comma should be included, as recommended by the ICZN code. Two or more authors of a name should be linked by an ampersand (&).

Place a single space between the author's last initial and surname and one space between the initials (e.g. Smith, E. A.).

References must be listed alphabetically by first author and chronologically at the end of the paper in the form:

Journal article

Shepherd, S. A. and Cannon, J. (1988). Studies on southern Australian abalone (genus *Haliotis*). X. Food and feeding of juveniles. *Journal of the Malacological Society of Australia* 9, 21–26.

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Book chapter

Kohn, A. J. and Amalsi, K. N. (1993). Comparative ecology of a biogeographically heterogeneous *Conus* assemblage. In 'The Marine Flora and Fauna of Rottnest Island, Western Australia'. (Eds F. E. Wells, D. I. Walker, H. Kirkman and R. Lethbridge.) pp. 523–538. (Western Australian Museum: Perth).

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A new *Littoraria* (Gastropoda : Littorinidae) from northwestern Australia

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Abstract

Littoraria ianthostoma, n. sp. is described from mangrove forests in Joseph Bonaparte Gulf in northwestern Australia. The new species superficially resembles the widespread *Littoraria articulata* (Philippi, 1846), with which it is sympatric, but differs in the closed penial sperm duct and absence of a pseudotrachea in the paraspermatozoa. Allozyme analysis confirms a large genetic distance between these two species and fixed allelic differences between sympatric samples. This discovery is surprising because the distribution and taxonomy of the mangrove-associated *Littoraria* of Australia had been considered well known. The anatomy and protoconch indicate that the new species produces pelagic egg capsules and undergoes planktotrophic development. Nevertheless, it has not been found outside Joseph Bonaparte Gulf and so appears to be the most narrowly distributed of the 39 members of the genus. Possible phylogenetic relationships of the new species and apparent isolation of Joseph Bonaparte Gulf are discussed.

Introduction

Recently one of us (MS) had the opportunity to take part in a research cruise to Joseph Bonaparte Gulf in northwestern Australia and made collections of littorinid molluscs as part of a study of molecular genetic variation within species. Among the material were two samples of a small *Littoraria* species from mangrove trees at Forsyth Creek (Northern Territory) and the Berkeley River (Western Australia). Superficially, the shells resembled those of *Littoraria articulata* (Philippi, 1846) and indeed the samples were microsympatric (intermingled on the same mangrove trees) with typical examples of that species. However, the shells were paler in colour, predominantly yellow or pink, and subtly different in shape. Anatomical examination and allozyme electrophoresis have confirmed that the two samples belong to a new species, here formally described.

This discovery is surprising because the genus has been the subject of modern taxonomic study and all 38 species hitherto known worldwide have been documented in detail (Reid 1986, 1999a, 2001). In particular, the Australian species had been considered well known because large amounts of material from the field and museum collections have been examined by both of us. The northwestern coast of Australia is one of the most inaccessible and biologically poorly explored regions in the country but, nevertheless, we have seen sufficient material from the Northern Territory and from Western Australia to suggest that the new species may be restricted to Joseph Bonaparte Gulf. This raises interesting questions about the biogeographic history of the area and possible causes of its isolation, and suggests that other narrowly endemic species might be sought there.

Phylogenetic relationships within the genus *Littoraria* have been studied by parsimony analysis of morphological characters (Reid 1986, 1989, 1999b). To assess the relationships of the new species we have added it to the dataset of Reid (1999b) and repeated the analysis.

Material and methods

Morphological study

Shell dimensions were measured with vernier calipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling; shell breadth (B) is the maximum dimension perpendicular to H; and the length of the aperture (LA) is the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shape was quantified as the ratios, H/B and H/LA (relative spire height, SH).

Living animals were fixed in 70% ethanol without prior relaxation. For general accounts of the male and female anatomy of *Littoraria*, see Reid (1986). The relative radular length was calculated as the total radular length divided by shell height. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 minutes, rinsing in distilled water, mounting on a film of polyvinyl acetate glue on glass, allowing to dry in air and coating with gold and palladium before examination in a scanning electron microscope. Unworn portions of radulae were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of teeth); at an angle of 45° from the front end of the radula (to show shapes of tooth cusps); and at an angle of 45° from the side of the radula (to show relief). The shape of the rachidian tooth was quantified as the ratio of the total length (in flat view) to the maximum basal width.

Allozyme analysis

Specimens of the new species were compared with *Littoraria articulata* using allozyme electrophoresis to examine variation at 12 loci. This comparison was performed because of the apparent morphological resemblance between the two species and because *L. articulata* is the only other *Littoraria* with which the new species occurs in sympatry and syntopy (intermingled on the same mangrove trees). In retrospect, our phylogenetic analysis suggests that these two species are not closely related, but the electrophoretic comparison provides an independent test of this conclusion.

Samples of 26 to 48 individuals of *L. articulata* were collected from six sites (Table 1), spanning the geographic range of the species within Australia. These included the two sites at which the new species was found. The new species was sampled from a single site, Forsyth Creek, and specimens included two morphs, one with a brown pattern on a white shell ($n = 14$) and the other lacking pattern ($n = 4$).

Samples were frozen alive in liquid nitrogen and stored at -80°C . Enzymes were extracted from both hepatopancreas and foot by grinding one volume of tissue with two volumes of grinding buffer (0.02M Tris-HCl pH 8, 0.25M sucrose, 0.1% (v/v) mercaptoethanol, 0.02% (w/v) bromophenol blue). Genetic variation of enzymes was examined by standard horizontal starch-gel electrophoresis using Tris-EDTA-borate (TEB), Tris-HCl, pH 8 (TC8) and Tris-maleate (TM) buffers and histochemical staining (Richardson *et al.* 1986; Murphy *et al.* 1996). Twelve enzymes representing twelve gene loci were examined: glucose-6-phosphate isomerase (EC 5.3.1.9; TC8 buffer; *Gpi* locus); glutamate oxaloacetate transaminase (EC 2.6.1.1; TM buffer; *Got*); hexokinase (EC 2.7.1.1; TM buffer; *Hk*); isocitrate dehydrogenase (EC 1.1.1.42; TC8 buffer; *Idh-2*); mannose-6-phosphate isomerase (EC 5.3.1.8; TEB buffer; *Mpi*); nucleoside phosphorylase (EC 2.4.2.1; TEB buffer; *Np*); peptidase (EC 3.4.11, EC 3.4.13; buffers TEB, TC8 and TEB; *Pep-A*, *Pep-D*, *Pep-E*); 6-phosphogluconate dehydrogenase (EC 1.1.1.44; TM buffer; *6Pgd*); phosphoglucomutase (EC 2.7.5.1; TM buffer; *Pgm-2*); and sorbitol dehydrogenase (EC 1.1.1.14; TC8 buffer; *Sdh*). Peptidases were detected using the following substrates: *Pep-A* with valyl leucine; *Pep-D* with leucyl proline; and *Pep-E* with leucine naphthylamide. Alleles at each locus were labelled numerically in order of electrophoretic mobility of their corresponding allozyme (proportional to the most common allozyme, with a designated value of 100). For enzymes encoded by two loci, these were numbered in order of decreasing mobility. Genetic similarities between all populations and across all 12 loci were quantified using Nei's (1978) unbiased genetic identity, which corrects for small sample sizes. The matrix of identities was summarised with a UPGMA phenogram.

Phylogenetic analysis

The morphological characters of the new species were coded and added to the dataset of Reid (1999b). Maximum-parsimony analysis of the data was performed with PAUP version 3.1.1 (Swofford 1993), using the same settings as Reid (1999b). The distribution of character states on the trees was examined using MacClade 4.0 (Maddison and Maddison 2000), with polychotomies interpreted as uncertainties in resolution.

Institutional abbreviations

AMS, Australian Museum, Sydney

BMNH, Natural History Museum, London

NTM, Museum and Art Gallery of the Northern Territory, Darwin

WAM, Western Australian Museum, Perth

Systematics

Family LITTORINIDAE Anon., 1834

Genus *Littoraria* Griffith & Pidgeon, 1834Subgenus *Littoraria* Griffith & Pidgeon, 1834

For diagnosis see Reid (1986, 1989) and for phylogeny, subgeneric classification and fossil history see Reid (1999b).

Littoraria (Littoraria) ianthostoma, n. sp.

(Figs 1A–F, 2A–F, I, J, 3A–F, 4)

*Material examined**Holotype.* AMS C.204871.*Paratypes.* 1 dry specimen, AMS C.204872; 5 dry specimens, BMNH 20010109; 25 specimens in ethanol BMNH 20010110; 2 dry specimens, NTM P18782; 2 dry specimens, WAM S12711.*Type locality:* Forsyth Ck, east coast Joseph Bonaparte Gulf, Northern Territory, Australia (14°56.5'S 129°23.5'E).*Other material examined.* 32 preserved specimens, type locality; 3 preserved specimens, Reveley Island, near mouth of Berkeley R., west coast Joseph Bonaparte Gulf, Western Australia, 14°22.7'S 127°45.5'E, BMNH 20010111; total of 5 penes; 2 sperm samples; 6 pallial oviducts; 2 radulae examined.*Diagnosis*

Shell small; columella excavated; usually a narrow pseudoumbilical area; 8–9 equally spaced primary spiral grooves on spire whorls; 16–19 low spiral ribs on last whorl, separated by deep narrow grooves. Shell colour polymorphic, yellow or orange-pink, with or without brown dashes on ribs; columella violet. Penis not bifurcate, filament half total length, glandular disc incorporated into base, sperm duct closed. Paraspermatozoa without pseudotrich. Development oviparous and planktotrophic.

Description

Shell (Fig. 1A–F). Adult size range 8.4–11.8 mm. Shape high-turbinata (H/B = 1.43–1.87; SH = 1.58–1.90); whorls rounded, suture impressed, periphery of last whorl slightly or not at all angled; moderate thickness. Sexually dimorphic; male shells a little smaller, slightly enlarged last whorl, more elongate aperture. Mature lip not flared; columella pillar relatively short, pinched and slightly excavated at base, producing basal knob; usually a narrow pseudoumbilical area between inner lip of aperture and columella pillar. Sculpture of 8–9 primary spiral grooves on spire whorls, almost equally spaced, posterior rib slightly narrower; most ribs flattened and undivided, separated by deeply impressed lines, but peripheral rib may become slightly raised and rounded on last whorl and adjacent grooves may reach one third of the rib width; 1–5 ribs at and below periphery of last whorl may be divided by a central line; total 16–19 ribs on last whorl; occasionally almost all ribs may be divided, producing up to 32 ribs on last whorl. Microsculpture of

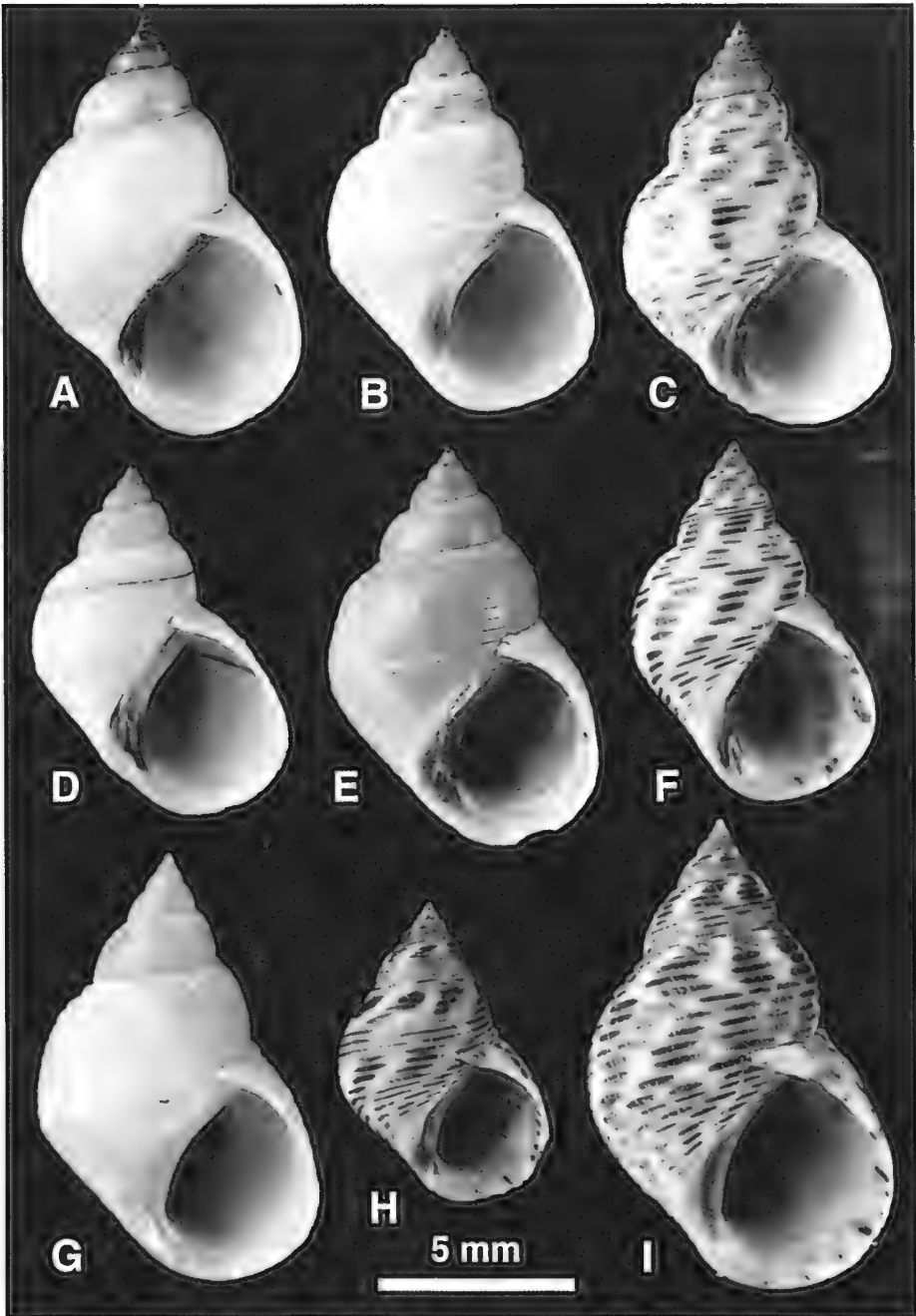


Fig. 1. *Littoraria ianthostoma*, n. sp. (A–F) and *Littoraria articulata* (Philippi, 1846) (G–I). A–F, Forsyth Creek, east coast Joseph Bonaparte Gulf, Northern Territory, Australia. A, C, D, E, Paratypes (BMNH 20010109). B, Holotype (AMS C.204871). F, Paratype (AMS C.204872). A–C, E, Females. D, F, Males. G, Female, Karratha Beach, Karratha, Western Australia (BMNH 20010113). H, I, Males, Forsyth Creek, east coast Joseph Bonaparte Gulf, Northern Territory, Australia (BMNH 20010112).

faint spiral striae over glossy rib surface, with axial microstriae in grooves. Protoconch diameter, 0.42 mm; about three whorls, with four spiral ribs and sinusigera notch. Colour polymorphic; ground colour white to pale yellow or rarely (one shell of 34) orange-pink; additional pigmentation usually faint and sparse; traces of brown pattern visible on most shells, but often restricted to apex or all spire whorls, leaving last whorl unpatterned; darkest shells with alternating brown and opaque white dashes on ribs, aligned in 8–10 axial series on last whorl; rarely (two shells of 34) a continuous brown line on shoulder of otherwise unpatterned last whorl. Columella purple-brown to dull violet; aperture yellow (or orange in single orange-pink shell) with traces of pattern showing through.

Animal. Head and sides of foot pale to dark grey; tentacles with dense narrow grey to black bands, unpigmented patch at inside of tentacle base. Operculum paucispiral, thin. Penis (Fig. 2A–D) long, not bifurcate; filament smooth, pointed at tip, half total length of penis, separated from wrinkled base by constriction; penial glandular disc incorporated into base just below junction with filament; penial vas deferens a closed tube to filament tip; penis unpigmented; vas deferens across head also closed (leading to closed prostate as in all *Littoraria* species). Paraspermatozoa (Fig. 2I, J) (observed after preservation in ethanol and therefore probably shrunk by up to 20%; Reid 1996: 6) 26–33 μm , with single large elongate fusiform rod body projecting from cell. Pallial oviduct (Fig. 2E, F) multispiral, 4.5 whorls, opaque capsule gland extending for 1.5 whorls; copulatory bursa in posterior position (beneath spiral portion of pallial oviduct). Egg capsules not seen, but pelagic capsules inferred from presence of large capsule gland (Reid 1986, 1989); development inferred planktotrophic from protoconch (Reid 1986, 1989). Radula (Fig. 3A–F) with relative radular length 0.85–0.94; rachidian length/width 1.00–1.13, base flared posteriorly, central cusp shield-shaped, flanked on either side by smaller pointed cusp and small or vestigial denticle; rachidian hood (additional anterior cutting edge) well developed; lateral with five cusps, central largest and bluntly rounded; inner marginal with four cusps; outer marginal with 3–4 cusps.

Habitat and distribution

Occurs commonly on the lower trunk and lower branches of *Avicennia marina* and occasionally *Rhizophora stylosa* trees on the seaward fringes of mangrove forests. The type locality, situated along the west bank of Forsyth Creek, is an area of intertidal mudflats approximately 50 m wide with scattered *A. marina* saplings and a few larger trees near the seaward edge. At this site, *L. articulata* was also common on the same mangrove trees as *L. ianthostoma* and barnacles covered the bases of the trunks. The only other arboreal gastropods found were scarce *Littoraria filosa* (Sowerby, 1832). Mangrove growth at the second collection site on Reveley Island was similarly sparse with scattered, stunted *A. marina* and *R. stylosa* trees growing on a stony beach. Again *L. articulata* was common and *L. filosa* uncommon on the same trees. So far *L. ianthostoma* has been recorded only from these two sites in Joseph Bonaparte Gulf (Fig. 4), approximately 200 km apart.

Etymology

Latin for 'violet-mouthed', in reference to the distinctive colouration of the columella.

Allozyme analysis

In the phenogram of genetic identities, the six populations of *L. articulata* form a group well separated from the sample of *L. ianthostoma* (Fig. 5). The genetic identity between the two species is 0.491, much lower than the identities among *L. articulata* populations

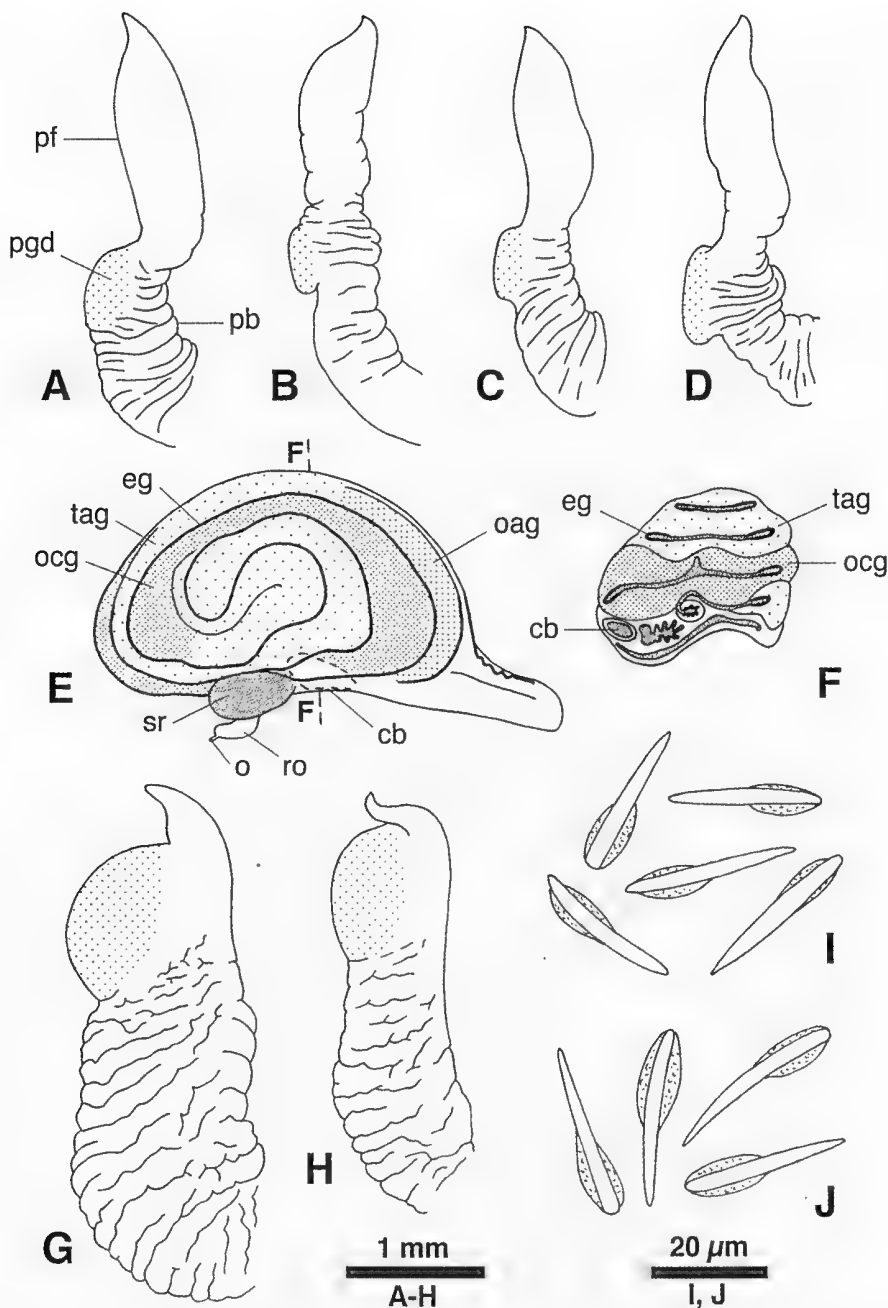


Fig. 2. Anatomy of *Littoraria ianthostoma*, n. sp. (A–F, I, J) and *Littoraria articulata* (G, H), Forsyth Creek, east coast Joseph Bonaparte Gulf, Northern Territory, Australia (A–F, I, J, paratypes BMNH 20010109, 20010110; G, H, BMNH 20010112). A–D, G, H, Penes. E, Pallial oviduct (with plane of transverse section F indicated). I, J, Paraspermatozoa from two specimens. Abbreviations: cb, copulatory burse (dashed outline, visible only by dissection or in section); eg, egg groove (heavy black line, visible by transparency due to black pigment); o, ovarian oviduct (leading from ovary); oag, opaque albumen gland (mid stipple); ocg, opaque capsule gland (dense stipple); pb, penial base (wrinkled); pf, penial filament (smooth); pgd, penial glandular disc (stipple); ro, renal oviduct; sr, receptacle (darkest stipple); tag, translucent albumen gland (light stipple).

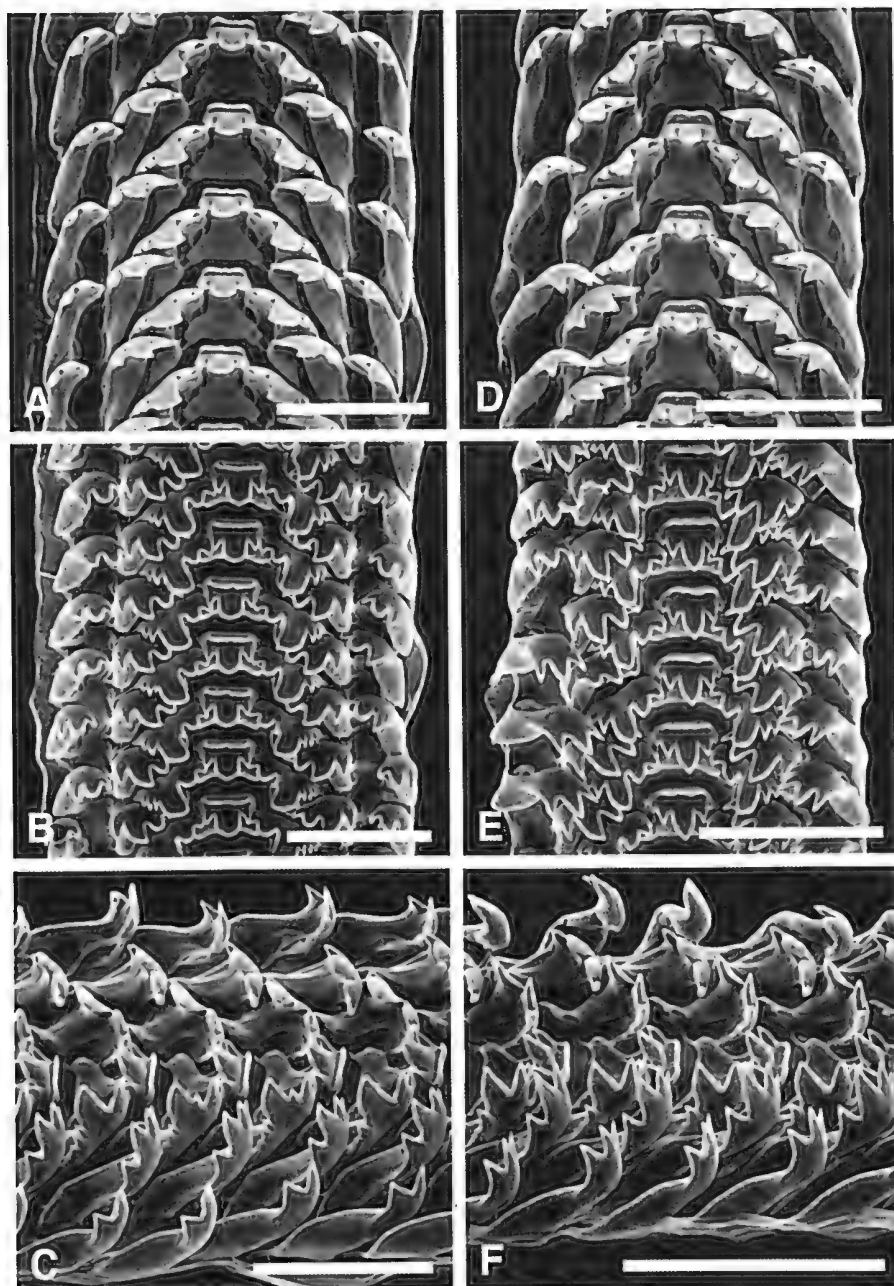


Fig. 3. Radulae of *Littoraria ianthostoma*, n. sp., Forsyth Creek, east coast Joseph Bonaparte Gulf, Northern Territory, Australia (BMNH 20010110). A–C, Female, shell H = 11.7 mm, three views: flat (A); 45° from anterior (B); 45° from side (C). D–F, Male, shell H = 9.0 mm, three views: flat (D); 45° from anterior (E); 45° from side (F). Scale bars: 100 μ m.

(0.974–0.997), even when these originate from opposite sides of the continent. There are fixed differences between the two species at four loci (*Hk*, *Pep-E*, *Np*, *6Pgd*) (Table 2). There are also differences at a further two loci with less than 10% overlap in allelic

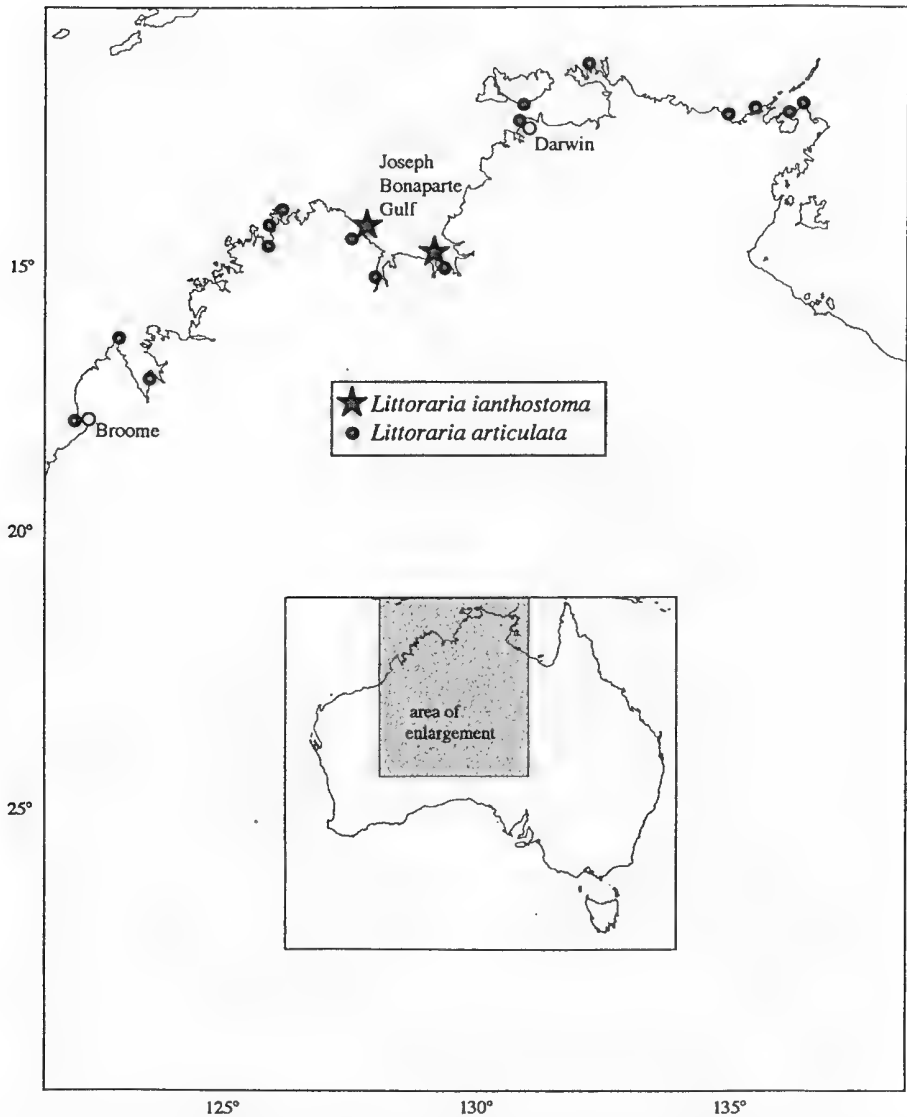


Fig. 4. Distribution of *Littoraria ianthostoma*, n. sp. For comparison, localities of examined samples of *L. articulata* from the vicinity are shown (museum collections in BMNH, AMS, WAM, details available from DGR on request). *Littoraria articulata* also occurs more widely throughout tropical Australia and Indo-Malaya (Reid 1986).

frequencies (*Pgm-2*, *Pep-A*) and, of the remaining six loci, both *Gpi* and *Idh-2* show alleles unique to one or the other species.

Discussion

In its shell characters, the new species closely resembles *Littoraria (Palustorina) articulata* (Philippi, 1846) (Fig. 1G–I), which is abundant on mangrove trees and sheltered rocky shores throughout the tropical coastline of Australia (Reid 1986). At both recorded sites for

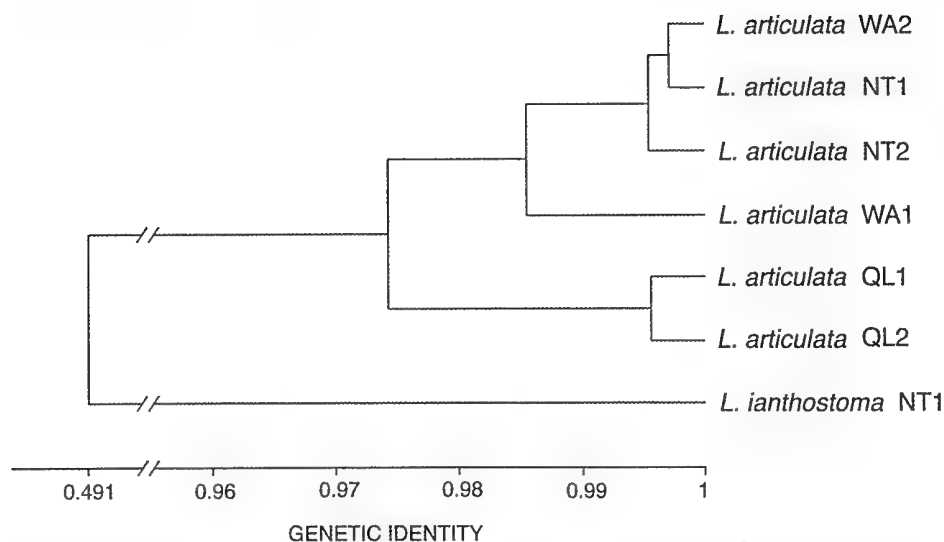


Fig. 5. Phenogram (UPGMA) of genetic identities (Nei 1978) of samples of *Littoraria articulata* and *L. ianthostoma*, n. sp. See Table 1 for locality abbreviations.

L. ianthostoma, the species occurs intermingled with *L. articulata* on the same mangrove trees. However, the similarity in shells is superficial, for there are anatomical differences sufficiently significant that, as discussed below, the two are classified in different subgenera. The allozyme analysis reveals a large genetic distance between these species and four loci at which there are fixed differences, even at the one site where both species were sampled. Even a single fixed allelic difference between sympatric samples provides strong evidence that they belong to different species, because it confirms the absence of interbreeding (Richardson *et al.* 1986).

The differences between *L. ianthostoma* and *L. articulata* are summarised in Table 3. Within Australia, confusion should not occur with any other *Littoraria* species (see Reid 1986). Shell outline, sculpture, microsculpture and aperture are almost identical in these two species. The most obvious shell character is the colouration, which, in the two available samples of *L. ianthostoma*, is strikingly polymorphic, most shells being yellow or faintly

Table 1. Localities of samples of *Littoraria articulata* and *L. ianthostoma*, n. sp. used in allozyme analysis

Species	Locality*	Latitude °S	Longitude °E	Code
<i>L. articulata</i>	Karratha Beach, Western Australia	20°34'	116°48'	WA1
<i>L. articulata</i>	Reveley Island, Berkeley River, Joseph Bonaparte Gulf, Western Australia	14°23'	127°46'	WA2
<i>L. articulata</i>	Forsyth Creek, Joseph Bonaparte Gulf, Northern Territory	14°57'	129°24'	NT1
<i>L. articulata</i>	Ludmilla Creek, Darwin, Northern Territory	12°24'	130°52'	NT2
<i>L. articulata</i>	Rowes Bay, Townsville, Queensland	19°14'	146°47'	QL1
<i>L. articulata</i>	Town of 1770, Queensland	24°10'	151°53'	QL2
<i>L. ianthostoma</i> , n. sp.	Forsyth Creek, Joseph Bonaparte Gulf, Northern Territory	14°57'	129°24'	NT1

Table 2. Allele frequencies at 12 loci in samples of *Littoraria articulata* and *L. ianthostoma*, n. sp. Localities coded as in Table 1. Mean sample sizes shown in parentheses.

Locus	Allele	<i>L. articulata</i>				<i>L. ianthostoma</i>		
		WA1 (47)	WA2 (42)	NT1 (26)	NT2 (46)	QL1 (47)	QL2 (45)	NT1 (17)
<i>Got</i>	130	0.052	—	—	—	0.042	—	—
	100	0.948	0.976	1.000	1.000	0.958	0.979	1.000
	70	—	0.024	—	—	—	0.011	—
	45	—	—	—	—	—	0.011	—
<i>Gpi</i>	105	0.012	—	0.019	0.011	0.097	0.129	—
	100	0.988	0.988	0.962	0.979	0.764	0.871	0.750
	95	—	0.012	0.019	0.011	0.139	—	0.167
	88	—	—	—	—	—	—	0.083
<i>Hk</i>	110	—	—	—	—	0.010	—	—
	100	0.990	0.988	1.000	1.000	0.990	1.000	—
	95	—	—	—	—	—	—	1.000
	80	0.010	0.012	—	—	—	—	—
<i>Idh-2</i>	145	0.106	0.024	0.058	0.053	0.042	0.053	0.083
	117	—	—	—	—	—	—	0.167
	115	0.021	—	—	—	—	—	—
	100	0.872	0.952	0.942	0.936	0.958	0.936	0.708
<i>Mpi</i>	85	—	—	—	—	—	—	0.042
	70	—	0.024	—	0.011	—	0.011	—
	110	—	0.012	—	0.051	—	—	—
	100	1.000	0.988	0.981	0.949	1.000	1.000	1.000
<i>Np</i>	90	—	—	0.019	—	—	—	—
	170	0.010	—	0.135	0.011	0.094	0.043	—
	160	—	—	—	—	—	—	1.000
	100	0.990	0.988	0.808	0.979	0.781	0.840	—
<i>Pep-A</i>	30	—	0.012	0.058	0.011	0.125	0.117	—
	110	—	0.060	—	—	—	—	—
	100	0.969	0.810	0.846	0.957	0.948	0.968	—
	85	0.021	0.131	0.154	0.043	0.052	0.011	0.583
<i>Pep-D</i>	80	0.010	—	—	—	—	0.021	0.389
	70	—	—	—	—	—	—	0.028
	150	—	—	—	—	—	0.022	—
	145	—	0.095	0.058	—	0.078	0.043	0.059
<i>Pep-E</i>	125	0.138	0.238	0.327	0.272	0.089	0.261	0.529
	110	0.191	0.202	0.154	0.283	0.300	0.326	0.412
	100	0.617	0.381	0.346	0.402	0.500	0.272	—
	85	0.032	0.083	0.115	0.022	0.033	0.043	—
	75	0.021	—	—	0.022	—	0.033	—
	130	—	—	—	—	—	—	0.393
	120	—	—	0.019	0.011	—	—	—
	112	0.074	0.061	—	0.032	0.031	0.064	—
	114	—	—	—	—	—	—	0.607
	108	—	—	—	0.021	—	0.021	—
	100	0.809	0.878	0.885	0.926	0.875	0.862	—
	86	0.117	0.061	0.096	0.011	0.083	0.043	—
	78	—	—	—	—	0.010	0.011	—

(continued next page)

Table 2. (continued)

Locus	Allele	<i>L. articulata</i>						<i>L. ianthostoma</i>
		WA1 (47)	WA2 (42)	NT1 (26)	NT2 (46)	QL1 (47)	QL2 (45)	NT1 (17)
<i>6Pgd</i>	170	—	—	—	—	—	0.011	—
	130	0.021	0.131	0.231	0.074	0.094	0.053	—
	125	—	—	—	—	—	—	1.000
	100	0.917	0.833	0.769	0.883	0.906	0.926	—
	85	0.031	0.036	—	0.021	—	0.011	—
	65	0.031	—	—	0.011	—	—	—
	45	—	—	—	0.011	—	—	—
<i>Pgm-2</i>	120	—	—	—	0.011	0.043	0.023	—
	115	0.229	0.107	0.096	0.191	0.032	0.068	—
	110	0.510	0.274	0.308	0.362	0.032	0.023	—
	100	0.229	0.619	0.462	0.426	0.883	0.875	0.056
	90	0.031	—	0.135	0.011	0.011	0.011	0.333
	85	—	—	—	—	—	—	0.611
<i>Sdh</i>	200	0.010	—	—	—	0.021	—	—
	150	0.042	—	—	0.043	0.021	—	0.031
	100	0.896	0.988	0.942	0.957	0.958	0.979	0.938
	60	0.052	0.012	0.058	—	—	0.021	0.031

patterned, others with brown dashes aligned in axial series and one of the available specimens (3%) is orange-pink. Shells of *L. articulata* are sometimes variable, but the great majority show a dark brown to black pattern of axially aligned dashes on a cream ground (the axial alignment often interrupted at the shoulder, Fig. 1H); yellow and lightly patterned shells are uncommon and the orange-pink colour is extremely rare (Reid 1986: 208). Apertural colouration shows subtle differences; in sympatric samples *L. articulata* has a pink or purple-brown columella, whereas that of *L. ianthostoma* is purple to violet, even in yellow shells lacking dark pattern on the outside of the shell. Further to the south west in its Australian range, *L. articulata* generally has a white columella (Fig. 1G). No anatomical characters have been found for the separation of females of *L. ianthostoma* and *L. articulata*. However, in males the form of the penis is diagnostic. The wrinkled base with

Table 3. Comparison of *Littoraria ianthostoma*, n. sp. and *L. articulata*

Character	<i>L. ianthostoma</i>	<i>L. articulata</i>
Shell colour	Polymorphic (yellow, orange-pink or brown-patterned)	Cream to yellow, with varying degrees of brown patterning, but very rarely plain yellow or orange-pink
Columella colour	Violet to purple	Pinkish- or purplish-brown, often white in NW Australia
Penis	Filament equal in size to wrinkled base, penial vas deferens a closed duct	Filament a small terminal appendage, penial vas deferens an open groove
Paraspermatozoa	Simple, lacking pseudotrach, rod bodies long and projecting	Pseudotrach present, oval rod bodies do not project from cell
Geographical distribution	Joseph Bonaparte Gulf	Indo-Malaya and throughout Australian tropics

integral glandular disc is similar in both, but in *L. articulata* (Fig. 2*G, H*) the filament is a small, pointed, terminal appendage, whereas in *L. ianthostoma* (Fig. 2*A–D*) it is equal in size to the entire penial base. In *L. articulata* the penial vas deferens is an open groove, but this is closed as a tube in *L. ianthostoma*. Paraspermatozoa are unlikely to be useful for identification purposes, but are of considerable phylogenetic significance, as discussed below. In *L. articulata*, the cells are 30–42 µm long, contain one or several oval rod bodies and bear a flagellum-like structure that is 170 µm long, called the pseudotrach (Reid 1986; Healy and Jamieson 1993; Buckland-Nicks *et al.* 2000).

Confusion is possible with several of the species of *Littoraria* known from other parts of the world. *Littoraria strigata* (Philippi, 1846) from South East Asia (see Reid 1986) and *L. sinensis* (Philippi, 1847) from China (see Reid 2001) are almost identical in shell characters to *L. articulata* and are separated from that species mainly by the relatively greater lengths of their penial filaments. Except for that one character, the differences listed in Table 3 therefore serve to distinguish *L. ianthostoma* from *L. strigata* and *L. sinensis*. Another similar species is *L. vespacea* Reid, 1986 from South East Asia; in that species the penis is of similar shape but with an open sperm groove, the rod bodies of the paraspermatozoa are short, the copulatory bursa is anterior and the shell is broader, distinctively patterned and not polymorphic (see Reid 1986). In the eastern Pacific Ocean, *L. rosewateri* Reid, 1999 has a polymorphic shell but the shape is narrower, the penis has a closed sperm duct like that of *L. ianthostoma* but the glandular disc is borne on a bifurcation of the base, and the bursa is anterior (see Reid 1999*a*).

The presence of shell colour polymorphism in *L. ianthostoma* is noteworthy. Elsewhere in the genus this character state has been recorded in three clades (Reid 1999*b*) and only in species found on the visually diverse backgrounds of mangrove foliage or marsh grass, not in species found on visually uniform mangrove trunks or rocks (Reid 1986, 1987). From this association it has been suggested that polymorphism may be adaptive in relation to visual selection by unknown predators. The available samples of *L. ianthostoma* are small and habitat details have been recorded at only two sites, so it is not known whether polymorphism is typical of the species and whether its usual habitat fits the trend observed in other species. An additional consideration is that in some bark-dwelling *Littoraria* species, shell colour is paler on some species of mangrove tree (*Avicennia* and *Sonneratia*, for example) than on *Rhizophora*, perhaps implying a direct ecophenotypic influence of substrate (Reid 1986).

The two radulae of *L. ianthostoma* that were examined show differences in cusp shape. This is common in the genus, in which both ontogenetic change and ecophenotypic plasticity have been reported (Reid 1999*a*; Reid and Mak 1999).

The phylogenetic relationships of *Littoraria* species remain poorly understood. Three phylogenetic analyses have been performed using an increasingly refined suite of morphological characters and resulting in a cladogram of the 36 species then recognised (Reid 1986, 1989, 1999*b*). All analyses agree that the genus is monophyletic, as supported by the synapomorphies: closed prostate gland; penial glandular disc; and lack of mamilliform penial glands (although none of these are unique in the family). Within the genus there are three moderately well-supported clades that have been given subgeneric status, *Protolittoraria*, *Littorinopsis* and *Palustorina*; the remainder form a paraphyletic and poorly resolved assemblage, the subgenus *Littoraria* (Reid 1999*b*). Of these subgenera, the most strongly supported is *Palustorina*, defined by the unique synapomorphy of the pseudotrach of the paraspermatozoa. The absence of this character state in *L. ianthostoma* excludes it from this clade.

In order to determine the phylogenetic relationships of *L. ianthostoma*, we added this new species to the morphological dataset used by Reid (1999b) and repeated the parsimony analysis. In the strict consensus tree (of more than 16000 trees, length 82 steps, consistency index = 0.524), *L. ianthostoma* appeared in the unresolved group of 14 members of the subgenus *Littoraria* (within clade three in Reid 1999b: fig. 4). In the 50% majority-rule tree it appeared (in 74% of the trees) as the sister-species of *L. (Littoraria) rosewateri*. This pair fell in a clade of western Atlantic and eastern Pacific species (clade five of Reid 1999b: fig. 4), united by the closed penial sperm duct. *Littoraria ianthostoma* also shares the synapomorphy of shell colour polymorphism with *L. rosewateri*. However, neither of these characters is unique within the genus, so this phylogenetic placement is not well supported.

Based on the weak criteria of overall resemblance and biogeographic proximity, another possible sister-species of *L. ianthostoma* is *L. (Littoraria) vespacea* from South East Asia. Similarities (possible synapomorphies) include the non-bifurcate shape of the penis (although the sperm channel is an open groove in *L. vespacea*) and the fusiform rod bodies of the paraspermatozoa (although these are not projecting in *L. vespacea*). At present there is insufficient information to speculate further on the phylogenetic relationships of the new species.

The geographic distribution of *L. ianthostoma* is interesting. It is well known that northwestern Australia is a region of marine endemism (Wells 1980, 1997). Among the Littorinidae alone, there are two other endemic *Littoraria* species (and two 'geographical forms', Reid 1986) and an endemic *Tectarius* (Rosewater, 1972). Nevertheless, the apparent restriction of the new species to Joseph Bonaparte Gulf is surprising. This might be a collecting artefact, since the region is relatively remote. However, we have examined abundant museum material of the morphologically and ecologically similar *L. articulata* from the vicinities of Broome and Darwin, and seven collections (89 specimens; BMNH, AMS, WAM) from between Cape Leveque and Vansittart Bay (Fig. 4) without discovering additional specimens of *L. ianthostoma*. This suggests that its distribution on the northwestern coast of Australia might indeed be restricted. If confirmed, this distribution would be the most restricted of any species in the genus. Nothing is known about the actual dispersal of *Littoraria* species. It is known (or inferred from protoconch characters) that all but one of the species have planktotrophic development and that most of these (excluding the ovoviviparous subgenus, *Littorinopsis*) produce pelagic egg capsules (Reid 1986, 1999a, 1999b, 2001). One species, *L. angulifera* (Lamarck, 1822), has an ampho-Atlantic distribution, implying dispersal in ocean currents over some 2000 km (Rosewater and Vermeij 1972; Merkt and Ellison 1998). On the other hand, Janson (1985) found some evidence for genetic isolation by distance among populations of *L. angulifera* from southern Florida. These species, including *L. ianthostoma*, would appear to have the potential for high dispersal and wide distribution, although whether this potential is realised may depend on other factors such as spawning behaviour, current patterns and coastal landforms.

It is not known whether the apparently restricted distribution of *L. ianthostoma* might reflect a general pattern of endemism and isolation of Joseph Bonaparte Gulf, or whether the species represents an isolated case of a relictual distribution. Reviews of oceanographic conditions (Bunt 1987) and of distribution patterns of marine fauna (Wilson and Allen 1987; Glasby *et al.* 2000) in northern Australia have not noted any peculiarity of the Gulf. However, a wider study of allozyme variation within *L. articulata* by one of us (MS, unpublished) hints at possible historical genetic isolation of the Gulf. Comparison of allelic frequencies among Australian populations has shown that the Forsyth Creek population

displays an unusual loss of rare alleles (18% compared with an average of 38%). The distribution of alleles can provide evidence of historical bottlenecks; populations at equilibrium accumulate rare alleles whereas those subject to bottlenecks lose them (Luikart *et al.* 1998). The 50% reduction of rare alleles in *L. articulata* from Forsyth Creek therefore suggests an historical reduction in gene flow in the area. Further suggestion of the uniqueness and isolation of the Joseph Bonaparte Gulf region has been provided by studies on fish assemblages, which have found that communities in the area are distinct from those in the nearby Arafura Sea (Saenger and Bucher 1989).

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Dietary preferences of two species of *Meridolum* (Camaenidae : Eupulmonata : Mollusca) in southeastern Australia

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Abstract.

Non-marine molluscs have extinction rates that rival the major vertebrate groups. Australia has about 800 described land snails, mostly endemic, yet virtually nothing is known of their biology, severely limiting effective conservation planning. In this study, a simple experiment was conducted to determine the feeding preferences of two native New South Wales species of camaenid snails, both with restricted distributions. Feeding experiments were conducted offering *Meridolum gulosum* (a rainforest species) and *Meridolum* sp. (a littoral rainforest species) several different types of living and senescent vegetation found in their natural habitat, as well as two species of commercially grown fungi. These experiments demonstrate that the camaenid snails studied show a preference for fungi over plant tissue but further experimental work is needed to examine feeding preferences for these and other land snails using an even greater range of potential food types.

Introduction

Non-marine molluscs, particularly land snails, are highly vulnerable: approximately 300 species world wide have been documented by the IUCN as becoming extinct over the last 300 years, an extinction rate that rivals that of vertebrates (Hadfield 1986; Cowie 1992; Yen and Butcher 1992; Baillie and Groombridge 1996; Ponder 1997; Seddon 1998). Land snails are an important component of Australia's biodiversity, comprising about 800 described, mostly endemic, species.

While it is often stated that invertebrates, including terrestrial molluscs, play a crucial role in ecosystem maintenance and function (e.g. Wilson 1987; Yen and Butcher 1992; Hadfield 1993), the details of the role of land snails in litter degradation in Australian ecosystems is unknown, as are virtually all other aspects of the biology of this diverse group.

One of the biological factors that govern the distribution of land snails is food type and availability (Little 1998). Pomeroy (1969) showed that by removing food from field plots, snails migrated to other areas where the food source was more readily available. Food availability can clearly influence distribution, abundance and habitat selection in land snails (Dillon 1980; Bishop 1981; Little 1998) and understanding the feeding biology of these animals is important if conservation management is to be successful. Diet also affects growth rates and some species of land snails have been observed to show increased growth when consuming their preferred food (Baur *et al.* 1994).

There is little information or literature that relates to the feeding habits and dietary preference of Australian pulmonates. Most species are referred to as detritivores and fungivores, which consume a variety of decaying plant material, algae and fungi, and there is often speculation that ground dwelling taxa are primarily fungal feeders (McLauchlan 1951; Colman and Burch 1977; Bishop 1981; Solem 1985; Smith and Stanicic 1998). However, these findings are generally the result of casual observation rather than critical study or experimentation.

The aim of this study was to examine feeding preferences of two land snail species endemic to the Illawarra area, south of Sydney, NSW, with the main objective to test whether these two species were preferential fungal feeders.

Materials and methods

Species studied

This study focused on two native land snail species endemic to southeastern Australia, *Meridolum gulosum* (Gould, 1864) and *Meridolum* sp. (unnamed species). These species are members of one of Australia's largest land snail families, the Camaenidae, and both are ground-dwelling snails found in rainforest remnants in the Illawarra region (Puslednik 1998).

Meridolum gulosum is large with a uniformly chestnut-coloured shell reaching an adult size of about 35 mm in diameter (Puslednik 1998). The head-foot is dark grey and the mantle, orange flecked with white. The umbilicus is generally closed to half closed. *Meridolum gulosum* ranges along the coast of NSW from Bulli to Batemans Bay, extending 40 km inland from the coast, with most records being centred around the Illawarra Region (Australian Museum collection; Allan 1950; Puslednik 1998).

Meridolum sp. is an undescribed species restricted to the littoral rainforest of Bass Point and two other locations around Lake Illawarra (Australian Museum collection). In this study, two shell morphs of this species were identified but were considered to be variants of a single species. *Meridolum* sp. is smaller than *M. gulosum*, with an average adult shell diameter of 23 mm. One morph of *Meridolum* sp. had similar shell and head-foot colouring to *M. gulosum*, while the other had a pale brown (almost yellow) shell and a light brown head-foot. Both morphs had an orange mantle flecked with white and an umbilicus that was half open to closed (Puslednik 1998).

Feeding trials: Meridolum gulosum

Ten individuals of *Meridolum gulosum* were collected from Bulli Pass (34°18'S 150°52'E), near Wollongong, NSW. Only adult snails were used in the trials. Each snail was housed separately in an empty, clean, sealed, 4-litre plastic container and was kept without food for 24 hours. After this period of starvation, faeces were removed and containers washed with water. Each snail was offered six different food types during the experiment, most collected from Bulli Pass subtropical rainforest within the area where the snails were found (food species used listed in Table 1). Plant species were selected on the basis of their abundance within the area. Living sapling leaves and dead mature leaves were offered as food in the trials as it was presumed that these items were accessible to this ground dwelling species. Native fungi proved too difficult to obtain in sufficient quantity, so two types of commercially grown fungi (*Agaricus bisporus* and *Pleurostus ostreatus*) were substituted.

Food samples were given to the snails as discs, cut into circles with a diameter of 21.5 mm (area = 363.1 mm²). Each food disc was positioned in a circle around the perimeter of the container, and a snail was placed into the middle of the container, equidistant from each food type. Containers were sprayed with water to prevent dehydration and small holes were punched into the lids of the containers to provide snails with air. After 24 hours, each snail was removed and the uneaten remains of food discs were collected. The amount of the different food types each individual consumed was recorded as a percentage, by measuring the area remaining and subtracting it from the initial area.

Feeding trials: Meridolum sp.

Slight modifications were made to the methods employed for *Meridolum gulosum*. Smaller plastic containers (2 litre) and smaller diameter food discs (diameter 14.5 mm, area = 165.1 mm²) were used. Two experiments were conducted with this species, each using ten different adult snails collected from Bass Point (34°34'S 150°53'E) on two separate occasions. The first was carried out as a pilot study to test the methods employed.

The first experiment offered six different living food types to *Meridolum* sp. (food species used listed in Table 1), while the second experiment was performed using six food types, a combination of both dead and living material (food species used listed in Table 1). Again the plant food types used were those found living within the habitat of the species and likely to be encountered by this snail species. Commercial fungi were again used because of the difficulty of obtaining native fungi. After 24 hours, each snail was removed, and the amount each individual consumed of the different food types was estimated and recorded as a percentage, as with the *Meridolum gulosum* experiment.

Data analysis

Data for each trial were analysed using a top-down concordance test (Zar 1999). Within each replicate, the food types offered were assigned a rank (a Savage score), according to the relative amount of each food type consumed within that replicate. This savage score was then used to calculate the concordance test statistic. The significance of this statistic was then assessed by comparison with the chi-squared distribution with $n-1$ degrees of freedom.

Results

Meridolum gulosum

Meridolum gulosum demonstrated a significant preference for fungi ($\chi^2_T = 32.05$, d.f. = 5, $P > 0.001$). Of the six different food types offered to *M. gulosum* only the two species of fungi were consumed. Every snail consumed all of the *Agaricus bisporus* offered and between 5 to 57% of the other fungus, *Pleurotus ostreatus* (Table 1). None of the other food types offered showed evidence of grazing (Table 1).

Meridolum sp.

Meridolum sp. demonstrated a significant preference for fungi in the first feeding trial ($\chi^2_T = 50.07$, d.f. = 5, $P > 0.001$). Of the six food types offered in this trial, only two were consumed: *Agaricus bisporus* (the only fungus offered in this trial) and *Tylophora barbata* (a sapling leaf). Every snail consumed all of the fungus and *Tylophora barbata* was consumed by only three of the ten individuals, with the amount consumed ranging from 8% to 63% (Table 1). None of the other food types offered showed evidence of grazing (Table 1).

In the second feeding trail, *Meridolum* sp. again showed a significant preference for fungi ($\chi^2_T = 29.67$, d.f. = 5, $P > 0.001$). In this trial four out of the six different food types were consumed, the two fungi (*Agaricus bisporus* and *Pleurotus ostreatus*), the sapling leaf of *Tylophora barbata* and the dead leaf of *Eucalyptus sieberi* (Table 1). Every snail consumed all of the *Agaricus bisporus* offered and between 10% to 100% of *Pleurotus ostreatus* (Table 1). *Tylophora barbata* was consumed by three individuals, the amounts consumed ranging from 11% to 100% (Table 1). Only one individual consumed the dead *Eucalyptus* sp., removing 21% of the amount offered (Table 1).

Discussion

Meridolum marshalli was observed to be a generalist omnivore by McLauchlan (1951), and captive animals were observed feeding on vegetable matter, plant tissue, decaying vegetation, fungus, and animal matter, although no choice experiments were conducted. Similarly, observations on captive *M. gulosum* indicated that this species will feed on various foods including vegetables, paper, leaves, soil and even commercial fish food (Puslednik 1998). However, the results of this study suggest that *M. gulosum* will feed on fungi in preference to living and dead leaves.

Among the northern Western Australian camaenids there is observational evidence of different feeding habits, *Ampliragada* species are generalist feeders of dead plant material and *Westraltrachia* species are also general plant feeders (Solem 1985). However, when species in these two genera are in sympatry, species of *Westraltrachia* apparently graze on algal-fungal blooms. *Meridolum gulosum* and *Meridolum* sp. do consume leaves. However, with only a single observation in this study of *Meridolum* sp. consuming dead vegetation and none for *M. gulosum*, it seems reasonable to assume that these taxa are not consumers of dead vegetation by preference. It appears that there may be significant differences in the

Table 1. Food types offered to *Meridolum gulosum* and *Meridolum* sp. during feeding trials, showing the mean percentage (\pm standard deviation, s.d.) consumed of each food type during each trial

<i>Meridolum gulosum</i> feeding trial 1 ($n = 10$)			<i>Meridolum</i> sp. feeding trial 1 ($n = 10$)			<i>Meridolum</i> sp. feeding trial 2 ($n = 10$)		
Name	Food type	Mean % consumed \pm s.d.	Name	Food type	Mean % consumed \pm s.d.	Name	Food type	Mean % consumed \pm s.d.
<i>Agaricus bisporus</i>	Fungus	100	<i>Agaricus bisporus</i>	Fungus	100	<i>Agaricus bisporus</i>	Fungus	100
<i>Pleurotus ostreatus</i>	Fungus	55 \pm 41	<i>Tylophora barbata</i>	Living sapling leaf	17 \pm 33	<i>Pleurotus ostreatus</i>	Fungus	77 \pm 37
<i>Acmena smithii</i>	Living sapling leaf	0	<i>Notolea ovata</i>	Living sapling leaf	0	<i>Acmena smithii</i>	Living sapling leaf	0
<i>Livistona australis</i>	Living sapling leaf	0	<i>Scopia braunii</i>	Living sapling leaf	0	<i>Tylophora barbata</i>	Living sapling leaf	12 \pm 31
<i>Acmena smithii</i>	Dead mature leaf	0	<i>Cissus antarctica</i>	Living mature leaf	0	<i>Acmena smithii</i>	Dead mature leaf	0
<i>Eucalyptus</i> sp.	Dead mature leaf	0	<i>Eucalyptus sieberi</i>	Living mature leaf	0	<i>Eucalyptus sieberi</i>	Dead mature leaf	2 \pm 7

feeding habits of camaenids, with some differences even seen between the two *Meridolum* species examined in this study. Experimental work is needed to verify observations of food preferences in other taxa. Other, non-camaenid, land snails have been shown to exhibit species-specific food preferences, even though they are capable of being generalists (Lawrey 1983; Baur *et al.* 1994; Heller and Dolev 1994; Desbuquois and Daguzan 1995; Gervais *et al.* 1997).

The strong dietary preference for fungi over plant tissue displayed by *Meridolum gulosum* and *Meridolum* sp. is important when considering fungus–invertebrate associations. Mammals have been identified as important in controlling and maintaining mycorrhizal relationships (see Johnson 1996 review) and it is possible that land snails may also play an important role. Fungus-feeding invertebrates with fungal associations have the ability to alter fungal species diversity, which may in turn affect the rate of leaf litter decomposition (Visser 1985). Invertebrates with strong preferences for particular fungi could alter fungal diversity by dispersing fungal spores (on the body or following passage through the gut) and selectively grazing fungus (Visser 1985).

The snails of this study showed preference for one of the two commercial fungi presented suggesting that selective grazing may be important. Ideally, experiments conducted using native fungi found in the habitat occupied by the snails need to be carried out. However, this will have considerable logistical difficulties given the rudimentary knowledge of native fungi and the presence of a large number of minute (such as moulds) or microscopic taxa. The trials in this study used only large fruiting bodies and it is not known whether the hyphae are consumed, or even accessible as a food source. In addition, future studies should examine other food types, including animal tissue, as observations of *Meridolum marshalli* feeding on animal tissue led McLauchlan (1951) to identify this species as an omnivore.

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A revision of the Australian Condyllocardiinae (Bivalvia : Carditoidea : Condyllocardiidae)

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Abstract

Nineteen species belong to the Condyllocardiinae in Australia, eighteen of these are endemic. Six genera are recognised: *Benthocardiella* Powell with two new species, *B. burtonae* n. sp. and *B. darwinensis* n. sp.; *Condyllocardia* Bernard with five species, one new (*C. cometa* n. sp.); *Condyllocuna* Iredale with four species, three new (*C. annieae* n. sp., *C. jimbecki* n. sp., and *C. tricola* n. sp.); *Cunanax* Iredale with four species; *Isodontocardia* n. gen. is monotypic, with one new species (*I. microcardia* n. sp.); and *Austrocardiella* n. gen. with three species, one new (*A. pouli* n. sp.).

Each species is illustrated and described from shell characters. Descriptions include full synonymy, subsequent references and habitat and distribution data. All type material relating to this revision is illustrated. The gross anatomy of *Condyllocardia notoaustralis* Cotton is described.

Three species have been excluded from *Condyllocardia* and the subfamily Condyllocardiinae: *Condyllocardia chapmani* is transferred to *Puyseguria*, ?Neoleptonidae; *Condyllocardia ovata* is transferred to *Mysella*, Galeommatidae *sensu lato*; and *Condyllocuna minuta* is transferred to Cuninae.

Introduction

The first records of species of Condyllocardiinae stem from Bernard's (1896, 1897a) descriptions of species from Stewart Island (New Zealand) and St Paul Island (South Central Indian Ocean). Bernard provided an excellent starting point for the definition of this group, as he included a very detailed description of hinge teeth, not only of the adult but also of embryos and juveniles. The features shared by this group are their small size, narrow hinge with a strong curved, ventrally directed, anterior right valve cardinal (CA3, following hinge teeth terminology of Bernard 1897a: fig. 3, here reproduced as Fig. 1), single anterior and posterior lateral in each valve and the small, centrally located internal ligament in a triangular to circular resilifer.

Roger and Lefebvre (1944) regarded the hinge teeth, rather than external ornamentation, as the most valuable generic and familial characters on the basis that many species with radial ornamentation pass through a juvenile phase where the shell only possesses commarginal ribbing.

Major aspects of the biology of condyllocardiines are unknown. Unconfirmed records indicate that they inhabit shallow water sandflats, where they may be abundant and possibly ecologically important (Slack-Smith 1998).

The anatomy of a condyllocardiine has not previously been described, although the presence of brooded embryos has been reported from the first descriptions of the family (e.g. Bernard 1896, 1897a, 1898). Recently the same mode of reproduction was recorded for Atlantic species (Salas and Rolán 1990; Salas and von Cosel 1991). It has been noted that the prodissoconch is generally large, ornamented with radial ribs or with an elevated nucleus, and generally with a strong bulging rim.

The earliest named Australian condyllocardiine is *Carditella subradiata* Tate, 1889 (Verco 1908a). The remainder were described after Bernard (1896) erected the family. Major contributions to the systematics of this group were by Cotton (1930), who described five new species, and Laseron (1953), who described seven. Lamprell and Healy (1998)

illustrated all the species described up to 1998 with copies of the original illustrations. The number of valid species names equalled the number of available names (25 names) until the present revision, in which there are 19 valid species and 12 synonyms and two species are excluded from the subfamily.

The family has a worldwide distribution, with the greatest known diversity in Australia. New Zealand has five species and three subspecies in *Benthocardiella*, one species and one subspecies in *Condylocardia* and three species in *Condyllocuna* (Spencer and Willan 1996). Eight species have recently been described from the Atlantic Ocean, four from the Cape Verde Islands (Salas and Rolán 1990) and four from West Africa (Salas and von Cosel 1991). Central American condyllocardiines include: *Condylocardia hippopus* (Mörch, 1861, p. 200) [synonym: *Condylocardia panamensis* Olsson, 1942 (p. 34)]; and *Condylocardia digueti* Lamy, 1916 (p. 443). One species (*Condylocardia io* Bartsch, 1915) described from South Africa is probably a *Benthocardiella*.

The following genera belong in the confamilial Cuninae, which is being revised separately: *Americuna* Klappenbach, 1963; *Carditopsis* Smith, 1881; *Carditella* Smith, 1881; *Carditellona* Iredale, 1936; *Cuna* Hedley, 1902; *Hamacuna* Cotton, 1931; *Mesocuna* Laseron, 1953; *Micromeris* Conrad, 1866; *Ovacuna* Laseron, 1953; *Particondyla* Laseron, 1953; *Propecuna* Cotton, 1931; *Saltocuna* Iredale, 1936; *Volupicuna* Iredale, 1936; and *Warrana* Laseron, 1953.

Materials and methods

The material contained in the research collection at the Australian Museum, Sydney (AMS) was used as the basis for the revision. This collection proved to be particularly useful because Hedley, Iredale and Laseron, who all worked with the condyllocardiines from Australia, had studied it. Additional material was borrowed from other museums. The abbreviations used are: AMS (Australian Museum, Sydney) (all numbers with the prefix C stem are from AMS); SAMA (South Australia Museum, Adelaide); TMH (Tasmanian Museum and Art Gallery, Hobart); NMV (Museum Victoria, Melbourne); WAM (Western Australia Museum, Perth); ANSP (Academy of Natural Sciences, Philadelphia); USNM (National Museum of Natural History Washington DC); NMNZ (Museum of New Zealand, Te Papa Tongarewa, Wellington); MNHN (Muséum National d'Histoire Naturelle, Paris); NTM (Northern Territory Museum and Art Gallery, Darwin); QM (Queensland Museum, Brisbane).

The small size of specimens in this group made it preferable to obtain scanning electron micrographs of the types. However, this was only done where the type material was syntypic and a lectotype could be selected for Scanning Electron Microscopy (SEM). No holotype or material from museums other than AMS was examined using SEM, but were photographed with a Pixera digital camera attached to a stereo microscope. Topotypic material was also used for SEM examination of the species. Where no material suitable for SEM was available from the type locality, specimens from the nearest possible locality were used. The shells were mounted on various sized stubs, gold coated, examined in a LEO SEM and digitally photographed.

Only one lot of wet material was available. The specimens were removed from their valves, cleared in glycerine and examined under a stereo microscope at 50–100× magnification.

A lectotype was selected and illustrated from syntype series throughout the manuscript. The lectotype selections are justified because they avoid future problems with defining the individual taxon name (e.g. caused by cryptic species) and illustrate the described species from multi-species type series.

Locality data (AMS and material from other museums) was exported from the collection database (TextPress) in Malacology, AMS, and plotted using ArcView. The abbreviations v and pr are used for valve and pair respectively and '+' indicates 'more than' the number indicated.

Shell characters (78) were defined and a data matrix created. Descriptions were generated using the DELTA program CONFOR (Dallwitz and Paine 1993).

The types and a few additional specimens were measured. The measurements were done with the aid of a graphics pad linked to a computer (see Ponder *et al.* 1989: 11). The length (SL) and height (SH) of the dissoconch, the length of the prodissoconch (PL) and the inflation of one valve (SI) were measured, and the inflation ratio (SL/SI×2) calculated.

Bernard and Munier-Chalmas (see Bernard 1898: 14; Cox *et al.* 1969: N52; Morton *et al.* 1998: 200–201; Middelfart 2000) proposed the most comprehensive hinge notation formula, which was based on

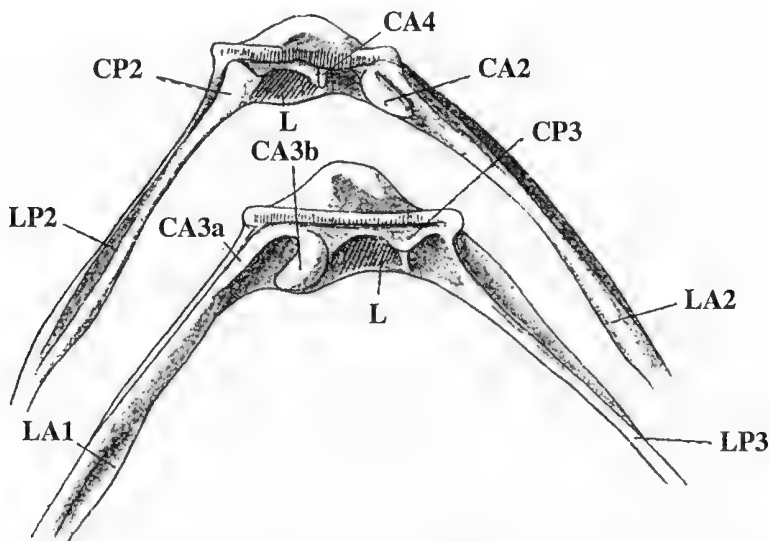


Fig. 1. The hinge teeth numbering system used by Bernard (1897a, reproduced from original publication). C, Cardinal; L in conjunction with letter and number, Lateral; L singularly, Ligament; A, Anterior; P, Posterior.

homologies of the lateral and cardinal teeth. As the formula is based on knowledge of the ontogeny of the hinge, ideally the ontogeny should be known for the formulation to be correctly applied. In the present revision, the work of Bernard (1896, 1897a) on Condyllocardiidae is the basis for the formulae used. The detailed description provided by Bernard (1897a, fig. 3, p. 187) has been the foundation for descriptions provided herein. Bernard's figure is reproduced in Fig. 1, with an additional indicator for CA4. Since Bernard only worked with a few species from *Condylocardia* and *Condyllocuna*, some extrapolation was necessary to cover the additional genera treated herein.

Key to species of Condyllocardiinae

- 1. Shell small, under 10 mm, triangular with small cup-shaped, rarely sculptured prodissoconch. Hinge teeth with prominent triangular cardinal tooth in right valve. Left valve with one prominent triangular or two diverging cardinals Cuninae
- Shell small, under 10 mm, triangular to oval, with large hat-shaped, smooth to sculptured prodissoconch. Right valve cardinal hook-shaped and merging with anterolateral, or with hinge teeth that appear similar in right and left valve (Condyllocardiinae).....2
- 2. Shell with commarginal ribs only.....3
- Shell smooth, with radial ribs or with radial and commarginal ribs.....9
- 3. Inner ventral margin denticulate.....4
- Inner ventral margin smooth.....5
- 4. Prodissococonch about 40% of dissoconch length. Shell almost equilateral.....
- *Condyllocuna annieae* n. sp.
- Prodissococonch about 30% of dissoconch length. Shell inequilateral..... *Condyllocuna projecta*
- 5. Prodissococonch more than about 50% of dissoconch length with one central depression6
- Prodissococonch less than 50% of dissoconch length with three radiating depressions7
- 6. Prodissococonch with about six commarginal ribs *Austrocardiella pouli* n. sp.
- Prodissococonch with about ten commarginal ribs *Austrocardiella isosceles*
- 7. Cardinal hinge teeth not visible as distinct elements *Condyllocuna tricola* n. sp.
- Cardinal hinge teeth visible and elaborate8
- 8. Prodissococonch with radial ribs (three radial indentations) and about three commarginal ribs.....
- *Austrocardiella trifoliata*
- Prodissococonch with small radial ribs, but no concentric ribs..... *Condyllocuna jimbecki* n. sp.

9. Shell smooth or with faint commarginal growth lines 10
 Shell with distinct sculpture 11
10. Shell transparent with pink tinge when fresh. Prodissoconch length about 0.36 mm, inflation ratio
 between 1.56 and 2.17 *Benthocardiella darwinensis* n. sp.
 Shell clear when fresh. Prodissoconch length about 0.44 mm, inflation ratio between 1.27 and 1.70 .
 *Benthocardiella burtonae* n. sp.
11. Shell with 7–8 radial ribs *Condylocardia cometa* n. sp.
 Shell with more than eight radial ribs 12
12. Shell strongly convex anterodorsally and posterodorsally, looks shouldered in lateral aspect.
 Prodissoconch small, cup-shaped and with five indentations or four radial ribs
 *Isodontocardia microcardia* n. sp.
 Shell not strongly shouldered, generally triangular in outline. Prodissoconch large and conspicuous in
 fresh shells 13
13. Prodissoconch D-shaped, central area raised and with two auricles (like a scallop). Right valve
 cardinal tooth anterior to ligament hook-like, curved ventrally 14
 Prodissoconch more or less circular; if fresh commarginal ribs may be observed 17
14. Up to 12 radial ribs. *Condylocardia limaeformis*
 More than 12 radial ribs 15
15. Shell inequilateral, displaced to halfway between posterior end and centre of shell.
 *Condylocardia pectinata*
 Shell equilateral or slightly inequilateral 16
16. Shell with flat radial ribs and deep interspaces. Anterodorsal and posterodorsal margins straight or
 weakly convex. *Condylocardia rectangularis*
 Shell with convex anterodorsal and posterodorsal margins, most prominent in larger specimens. Shells
 in some areas (south NSW coast) brown or mixture of brown and white
 *Condylocardia notoaustralis*
17. Shell with strong concentric sculpture crossing radial ribs. Large shells (5–6.5 mm) very solid. Right
 valve with two large triangular cardinal teeth anterior and posterior to the central ligament. Left
 valve with one anterior and one posterior conspicuous cardinal, and two small lamellate cardinals
 proximal to ligament. *Cunanax pisum*
 Concentric shell sculpture not conspicuous. Cardinal teeth either very long and diverging or small and
 similar looking in right and left valve. 18
18. Cardinals small, right and left valve hinges similar. 12–16 radial ribs *Cunanax subradiata*
 Cardinals large and elongate. More than 20 radial ribs 19
19. Shell with wide hinge plate, cardinal teeth at less than 45 degrees to dorsoventral plane. Radial ribs
 between 20 and 24 *Cunanax crassidentata*
 Shell with narrow hinge plate, cardinal teeth at more than 45 degrees to the dorsoventral aspect. Max.
 21 radial ribs *Cunanax compressa*

Systematics

The present revision concerns the Australian genera of Condylocardiinae. The cunine genera *Micromeris* Conrad, 1866, *Mesocuna* Laseron, 1953 and *Particondyla* Laseron, 1953 were included in the Condylocardiinae by Chavan (1969), but they do not belong in this subfamily and are therefore excluded from this treatment (see Introduction).

Family CONDYLOCARDIIDAE Bernard, 1896

Diagnosis

Shells minute, generally under 2 mm, few up to 9 mm, trigonal to broadly ovate, commonly higher than long; radial ribs more or less marked, may be hidden by concentric sculpture or internal in shells. Ligament internal. Hinge teeth: CA3 dorsally curved into CA3a, CA3b, the latter being enlarged. Two laterals in each valve, each longer than half length of dorsal anterior and posterior slopes. Pallial line simple, adductor muscles isomyarian.

Remarks

The obliteration of the hinge tooth CA4 used in the diagnosis of Condyllocardiidae by Chavan (1969) is not a consistent character for the whole family or either of the two subfamilies. Chavan's description of a CA5b to CA6b (5b–6b in text) as posterior to the ligament or CA4 is perplexing. The posterior cardinal in the left valve (here interpreted as CP3) is fused to the long posterior lateral, but has nothing to do with CA5b or CA6b.

Subfamily **CONDYLOCARDIINAE** Bernard, 1896*Diagnosis*

Prodissoconch large, conspicuous and, in some species, sculptured. Hinge teeth: CA5 generally absent, if present directed anteroventrally. CA4b directed posteroventrally if not vestigial.

Remarks

The diagnosis by Chavan (1969) does not provide any solid distinction between the condyllocardiines and the cunines. The prodissoconch size and shape is a very good character for the condyllocardiines, despite one species having a small, slightly sculptured prodissoconch closely similar to the cunines. The CA5, characteristic of Cuninae, is found in one genus in the condyllocardiines, but here directed anteroventrally, not posteroventrally as in the cunines. The cardinal CA4b is present in a few genera, but directed anteroventrally, not ventrally or posteroventrally as in the cunines. The difference between characters of the cunines and condyllocardiines does not seem to call for separation at the family level.

Genus *Condylocardia* Bernard, 1896

Hippella Mörch, 1861: 199, invalid (*nomen oblitum*) ICZN opinion 872, 1969: 216. Type species (monotypy): *Hippella hippopus* Mörch, 1861: 200.

Condylocardia Bernard, 1896: 195. Type species: *Condylocardia santipauli* Munier-Chalmas in Bernard, 1896: 196, invalid emendation to *Condylocardia pauliana* by Bernard (1897a: 11). Moore's (1969) statement that the type selection was by subsequent designation of Cossmann (1902: 23) is in error, since Bernard (1897a: 11) unequivocally designates *Condylocardia pauliana* 'Espèce type de genre'.

Radiocondyla Iredale, 1936: 272. Type species (original designation): *Radiocondyla arizela* Iredale, 1936 (= *Condylocardia rectangularis* Cotton, 1930).

Diagnosis

A condyllocardiine with shell less than 2.5 mm in length, triangular to oval; prodissoconch auricular, with central raised area and faint radial ribs. Dissoconch with radial ribs, ventral margin dentate. Hinge teeth: CA3 curved into CA3a,b; CA2 undivided and free.

Remarks

A syntype (no. 5) of *C. pauliana* from MNHN has been examined, and is here illustrated (Fig. 2). The specimen is slightly eroded but not so much as to obscure the generic characters. *Condylocardia pauliana* is very similar to *C. crassicosta* Bernard, 1896 from New Zealand and *C. limaeformis* Cotton, 1930 from Australia (see below). With only one syntype valve of *C. pauliana* available for comparison with *C. crassicosta* it is unclear whether they are conspecific.

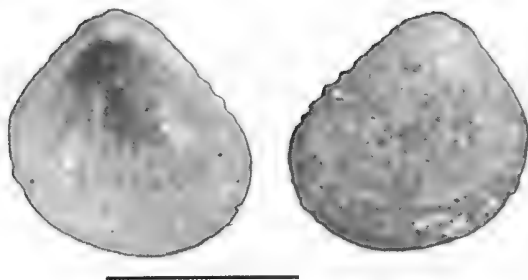


Fig. 2. *Condylocardia pauliana*. Syntype V, St Paul Island, South Indian Ocean. Scale bar: 1 mm.

Iredale (1936) used the closely set hinge teeth, flat radial ribs and larger size to distinguish *Radiocondyla* from *Condylocardia*, basing *Condylocardia* on *C. porrecta* (= *Cunanax subradiata*). These characters are, however, not sufficiently distinct from other members of *Condylocardia* to justify a separate genus.

Condylocardia cometa n. sp.

(Figs 3a–e, 5)

Material examined

Holotype. C379938 (1v) (Fig. 3a, d, e) SE of King Is., Bass Strait, Tasmania, 40°10.5'S 144°18.6'E, 51 m, 24 April 1973, coll. M. T. Sprightly.

Paratypes. C379940 (2v) (Fig. 3b, c) NW of Sandy Cape, Tasmania, 41°9.4'S 144°10.6'E, 132 m, 14 April 1973, coll. M. T. Sprightly.

Other material examined. **Tasmania**. W of Port Davey, 43°20.3'S 145°48.2'E, 82 m, 9 April 1973, C379939 (1v).

Description

Shell. Maximum length 1.35 mm, maximum height 1.34 mm, equilateral, orthogyrate, translucent or opaque white. Inflation ratio, 1.45–1.82.

Prodissoconch. Maximum length 390 μ m, consisting of prodissoconch I and II. Prodissoconch I with one central indentation, prodissoconch II with slight radial pattern, rim sharp. Anterior and posterior prodissoconch auricles present.

Dissoconch. Lunule and escutcheon short, narrow with commarginal sculpture. Outline triangular, anterior and posterior end angled. Anterior and posterior dorsal slopes flat or very weakly convex, ventral margin concave. External sculpture of few major erratic and numerous fine growth lines, 7–8 strong radial ribs. Inner margin denticulate with 6–9 denticles. Hinge plate narrow and short. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral (LPIII, LPII) long. Right valve anterior cardinal tooth (CA3) strongly arched, divided into anterior cardinal teeth elements CA3a,b. Posterior cardinal tooth (CP3) small, divided into elements CP3a,b. Left valve anterior cardinal teeth (CA2 and CA4) present, cardinal tooth CA4 divided dorsally into teeth elements CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP2 the largest. Internal ligament 50 μ m long, rounded, in resilium.

Dimensions. See Table 1.

Distribution

Western Tasmania; on continental shelf, 51–131 m. Habitat unknown. This species is only known from shells.

Table 1. Measurements of specimens of *Condylocardia cometa* n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condylocardia cometa</i> , holotype, C379938	1.00	1.00	0.33	0.29	1.72
<i>Condylocardia cometa</i> , paratypes, C379940 (Fig. 3b)	1.19	1.17	0.32	0.37	1.61
(Fig. 3c)	1.13	1.01	0.34	0.31	1.82
<i>C. cometa</i> , C379939	1.33	1.34	0.39	0.46	1.45

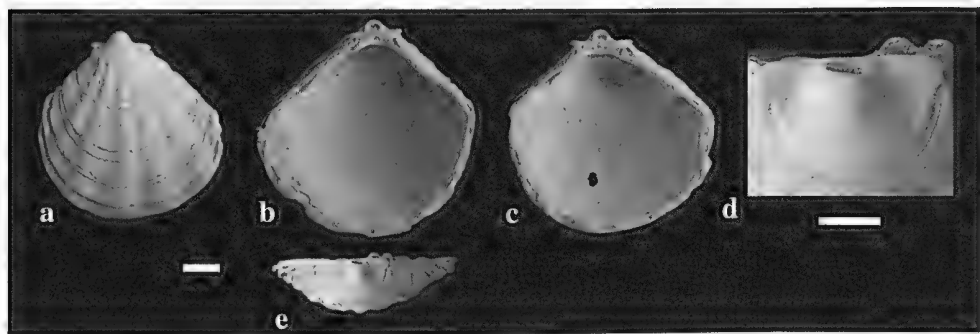


Fig. 3. *Condylocardia cometa* n. sp. Holotype C379938, SE of King Is., Bass Strait, Tasmania, a, d, e. Paratypes C379940, NW of Sandy Cape, Tasmania, b, c. Scale bars: a-c, e, 200 µm; d, 100 µm.

Remarks

Condylocardia limaeformis Cotton, 1930 is closely similar to this species. The fewer radial ribs (7–8 instead of 9–12), the angled anterior and posterior ends and the equilateral beaks separate shells of *C. cometa* from *C. limaeformis*.

Etymology

From Latin *cometa* meaning ‘a comet’.

Condylocardia limaeformis Cotton, 1930

(Figs 4a–p, 5)

Condylocardia crassicosta Bernard, 1897a. Verco, 1908a: 360. – Gatliff & Gabriel, 1909: 46; May, 1909: 54, pl. 6, fig. 6; May, 1921: 14; May, 1923: pl. 7, fig. 9; Macpherson & Gabriel, 1962: 321 (not Bernard, 1897a).

Condylocardia limaeformis Cotton, 1930: 238, fig. 12 (type locality: Cape Borda, South Australia, 113 m. Holotype, SAMA D.10112 (1v) (Fig. 4a)). – Lamprell & Healy, 1998: 168, fig. 472.

Condylocardia adelaideana Cotton & Godfrey, 1938: 194, fig. 195 (type locality: Backstairs Passage, South Australia, 40 m. Holotype, SAMA D.12609 (1v) (Fig. 4b), paratypes, SAMA D.12610 (3pr, 2v)). – Macpherson & Chapple, 1951: 17; Kershaw, 1955: 296.

Radiocondyla adelaideana (Cotton & Godfrey, 1938). Cotton, 1961: 207, fig. 201. – Lamprell & Healy, 1998: 172, fig. 498.

Condylocardia kunopia Laseron, 1953: 39, figs 10, 10a (type locality: Narrabeen Beach, Sydney, New South Wales, 33°42'S, 151°18'E, Pre 1951, coll. C. F. Laseron. Lectotype (here selected), C090557 (1v) (Fig. 4c), paralectotypes C388179 (2v)). – Iredale & McMichael, 1962: 17; Jansen, 1995: 101, fig. 423; Lamprell & Healy, 1998: 168, fig. 475.

Condylocardia sp. Laseron, 1953: 39, 12, 12a.

Other material examined. **New South Wales.** *Sydney area:* Off Chinaman's Beach, 33°48.97'S 151°14.87'E, 3.5–7.5 m, 1967, C379891 (1v); Balmoral Beach, 33°49.7'S 151°15.03'E, 1957, C366855, (1v); Little Coogee Bay, 33°55.25'S 151°15.7'E, 21 April 1895, C379901 (1pr); same locality, 19 July 1895, C379903 (1pr); Bate Bay, Cronulla Beach, 34°2.5'S 151°10'E, 1967, C379934 (13v); Gunnamatta Bay, 34°3.95'S 151°8.55'E, 4 Sep. 1926, C347816 (1v). Werri Beach, Gerringong, 34°44.3'S 150°50'E, beach, 1950, C366858 (4v). Sussex Inlet, Wreck Bay, 35°11'S 150°35'E, 1955, C366851 (1v). Pebbly Beach, 35°36.8'S 150°19.7'E, 1980, C366852 (3v). Batemans Bay, 35°43'S 150°12'E, shell sand on beach, 1950, C366853 (3v). Broulee, near Moruya, 35°51.5'S 150°10.5'E, 1985, C379890 (2v). Bermagui, Shelly Beach, 36°25'S 150°5'E, 1967, C366857 (28v). Eden Harbour, 37°4.45'S 149°54.5'E, 1955, C366856 (16v). Twofold Bay, 37°5'S 149°54'E, 27–46 m, 1953, C315615 (1v). Twofold Bay, 37°5'S 149°54'E, shore material, 1919, C366854 (4v). Boydtown, Twofold Bay, 37°6'S 149°53'E, beach, 1965, C379937 (1v). **Victoria.** Mallacoota, 37°34'S 149°56'E, 1918, C50489 (7v). Bass Strait, 44 km S of Marlo, 38°12'S 148°35'E, 146 m, flat outer shelf, 7 May, 1969, C379895 (2v). Between Eagle and Crawfish Rock, North West Arm, Western Port, 38°16'S 145°17'E, 3.6–5.5 m, 15 Feb. 1969, C379894 (1pr). Sandy Point, Western Port, just N of North Arm, 38°24.3'S 145°14.2'E, 7.5 m, sandy mud and shell, 28 Feb. 1977, C379896 (3v). Port Phillip, Frankston, 38°9'S 145°10'E, 1910, C30193 (2pr). Port Phillip Bay, Macrae, 38°20.9'S 144°55.5'E, 1967, C379902 (1v). Portarlington, Port Phillip Bay, 38°7'S 144°39'E, on *Galeolaria*, 22 March 1975, C379904 (1v). **Tasmania.** Blythe (Siding), near Burnie, 41°5'S 146°E, March 1956, C379905 (2v). Sulphur Creek, between Penguin and Burnie, 41°6'S 146°2'E, C379900 (28v). Goat Is., Ulverstone, 41°8'S 146°8'E, Rat-tailed *Caulerpa* in large rockpools, 20 Feb. 1984, C379893 (1v). Goat Is., W of Ulverstone, 41°8'S 146°8'E, short brown algae in pool, intertidal rocks, 18 March 1975, C379898 (1v). Maria Is., 4 km NE Beaching Bay, 42°27.5'S 148°12'E, 82.5 m, 25 March, 1970, C379914 (9v). Frederick Henry Bay, 42°53'S 147°34'E, 1908, C29421 (4v). Tinderbox Bay, S of Hobart, 43°3'S 147°20'E, 15 m, 1955, C379899 (14v). S of D'Entrecasteaux Channel, 43°40.4'S 146°50.4'E, 104 m, 2 April 1973, C379892 (20v). **South Australia.** Adelaide, Outer Harbour Beach, 34°49'S 138°29'E, 1957, C379911 (3v). Gulf St. Vincent, Largs Bay, 34°49'S 138°29'E, 1967, C379913 (2v). Bluff Beach, Yorke Peninsula, 34°44'S 137°29'E, rocks on intertidal limestone bench, 23 Feb. 1985, C379907 (2v). Spencer Gulf, Hardwicke Bay, 34°45'S 137°18'E, sand, 1902, C13447 (2v). Kangaroo Island, Stokes Bay, 35°37'S 137°12'E, stones on sheltered boulder shore, low tide, 4 March 1978, C379906 (4v). Spencer Gulf, Tumby Bay, 34°22'S 136°8'E, 1967, C379921 (28v). Fisherman Point, Cape Donnington, 34°45.5'S 135°59'E, stones in sheltered intertidal rocks, C379909 (2v) and in coralline turf on sheltered intertidal rocks, C379910 (1pr), 14 Feb. 1985. **Western Australia.** *Off Esperance:* 34°22.9'S 121°3.5'E, 85 m, coarse shell sand, Feb. 1981, C379919 (1v); 34°1.8'S 121°1.8'E, sand, 3 Feb. 1981, C379918 (3v). Two Mile Beach, Hopetoun, 33°57'S 120°7'E, 9 Jan. 1975, C379920 (1v). *Off Albany:* 35°14.4'S 118°20.5'E, 75 m, sand and shell, 12 March 1980, C379916 (1v); 35°6.4'S 118°10.6'E, 72 m, fine sand, 12 March 1980, C379915 (1v); 35°9.1'S 117°49'E, 64 m, coarse sand, 13 March 1980, C379917 (1v).

Description

Shell. Maximum length 1.43 mm, maximum height 1.49 mm, slightly inequilateral, orthogyrate, transparent to opaque white. Inflation ratio, 1.29–2.02.

Prodissoconch. Maximum length 360 µm, consisting of prodissoconch I and II. Prodissoconch I with one central indentation, prodissoconch II with slight radial pattern and sharp rim. Anterior and posterior prodissoconch auricles present.

Dissoconch. Lunule and escutcheon smooth, short and narrow. Outline triangular, anterior and posterior end angled. Anterior and posterior dorsal slopes straight or weakly convex. External sculpture of fine commarginal growth lines and 9–12 strong radial ribs. Inner margin denticulate, with 9–12 denticles. Hinge plate narrow and short. Two smooth lateral teeth present in each valve. Right and left valve anterior lateral tooth (LAI, LAII) and posterior lateral tooth (LPIII, LPII) long. Right valve anterior cardinal tooth (CA3) strongly arched, divided into anterior cardinal elements CA3a,b. Posterior cardinal tooth (CP3) present, divided into elements CP3a,b. Left valve anterior cardinal teeth (CA2 and CA4) present, CA4 divided into elements CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP2 the largest. Internal ligament, 80 µm long, rounded, in resiliium.

Dimensions. See Table 2.

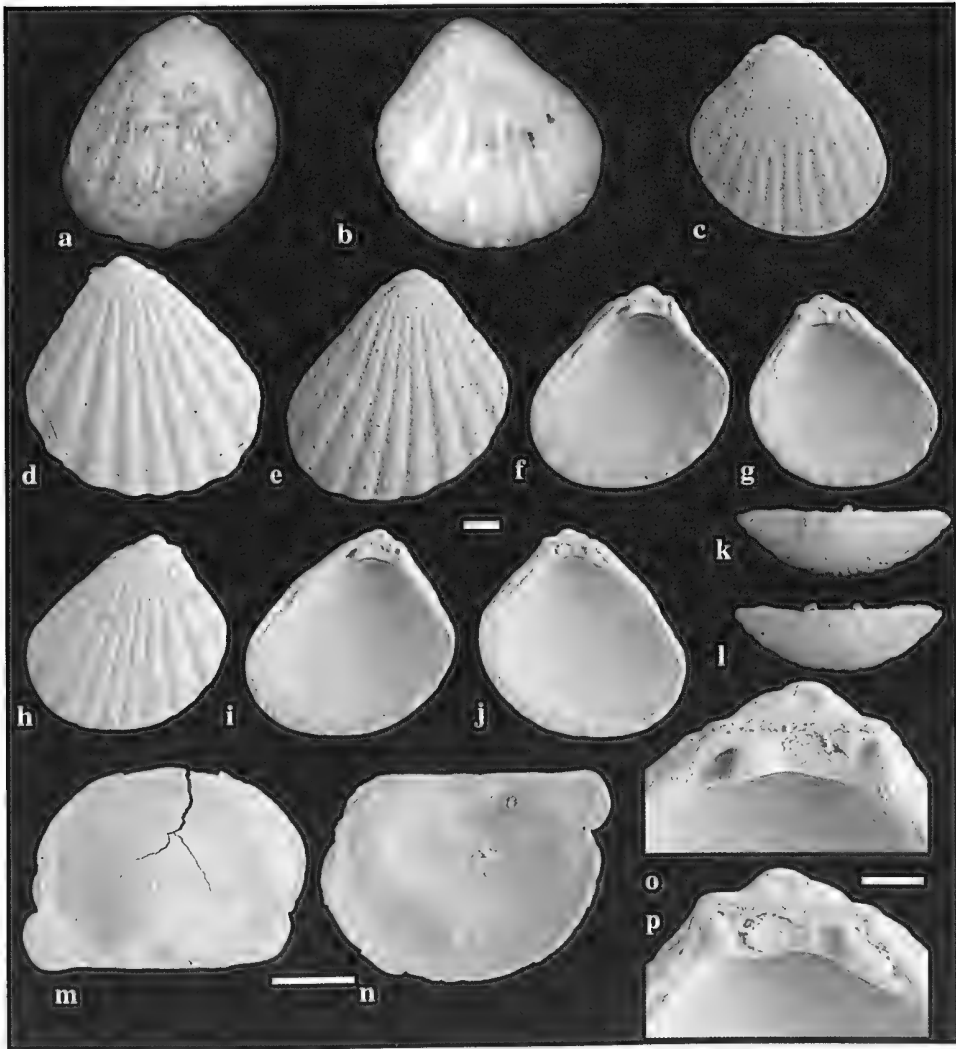


Fig. 4. *Condyllocardia limaeformis*. *a*, *Condyllocardia limaeformis* holotype SAMA D.10112, Cape Borda, South Australia. *b*, *Condyllocardia adelaideana* holotype SAMA D.12609, Backstairs Passage, South Australia. *c*, *Condyllocardia kunopia* lectotype C090557 Narrabeen Beach, Sydney, New South Wales. *d*, C379906, Kangaroo Island, South Australia. *e*–*g*, C379934, Cronulla, New, South Wales. *h*–*p*, C366856 Eden, New South Wales. Scale bars: *a*–*l*, 200 µm; *m*–*p*, 100 µm.

Reproduction

One embryo observed in each of two dried specimens.

Distribution

Mid New South Wales south to Victoria, Tasmania, South Australia and southwestern Western Australia; from intertidal rock pools to 146 metres. Shells have been collected intertidally in turfing algae, under stones, in sand or from shelly bottoms. This species is only known from shells.

Table 2. Measurements of specimens of *Condylocardia limaeformis* Cotton, 1930

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condylocardia limaeformis</i> , holotype, SAMA D.10112 (Fig. 4a)	1.29	1.37	0.28	0.50	1.29
<i>Condylocardia adelaideana</i> , holotype, SAMA D.12609 (Fig. 4b)	1.29	1.23	0.32	-	-
<i>Condylocardia kunopia</i> , lectotype, C090557 (Fig. 4c)	1.13	1.14	0.40	0.28	2.02
<i>Condylocardia limaeformis</i> , C379921	1.24	1.22	0.36	0.34	1.82
	1.29	1.29	0.35	0.44	1.47
	1.43	1.49	0.36	0.49	1.46
	1.20	1.15	0.33	0.41	1.46
	1.13	1.19	0.34	0.38	1.49

Remarks

The holotype of *C. limaeformis* is a very eroded valve but recognisable as belonging to this taxon. The lectotype of *C. kunopia* is quite inflated compared to other measured material, but this is merely an indication of the shape variation in *C. limaeformis*. *Condylocardia pauliana* from St Paul Island and *C. crassicosta* from Stewart Island, New Zealand are morphologically very similar to specimens of this species but available material of *C. crassicosta* seems slightly stouter and has heavier hinge teeth than *C. limaeformis*. It seems likely that these three taxa, ranging from St Paul Island to Australia and New Zealand, have a common ancestry and may even be geographically isolated populations of one species.

As the distribution indicates (Fig. 5), there are disjunct concentrations of records. This is probably due to differing sampling intensity but may also be due to lack of appropriate habitat exposure, or even the existence of cryptic species.

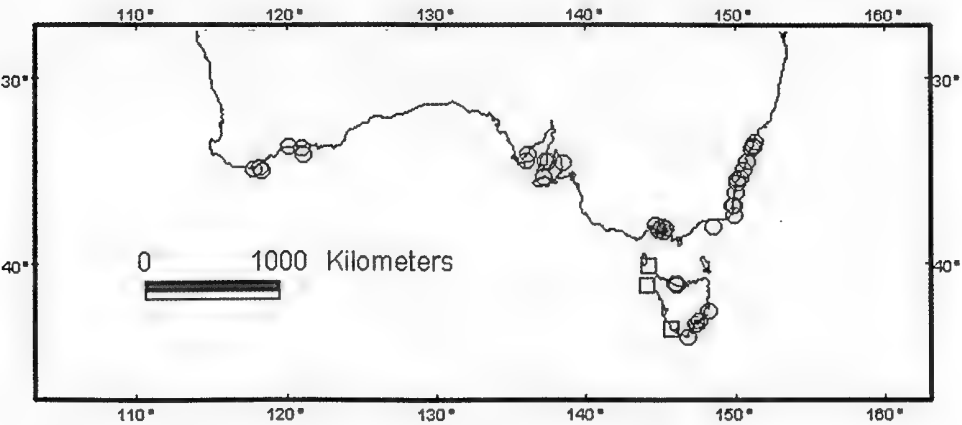


Fig. 5. Distribution of *Condylocardia limaeformis* (O) and *C. cometa* n. sp. (□).

Condyllocardia notoaustralis Cotton, 1930

(Figs 6a–p, 7A, B, 8, 9)

Condyllocardia australis Bernard, 1897a. – Verco, 1908a: 360; Gatliff & Gabriel, 1912b: 173; Macpherson & Chapple, 1951: 17 (not Bernard, 1897a).

Condyllocardia notoaustralis Cotton, 1930: 239, fig. 13 (type locality: off Beachport, South Australia, 366 m. Holotype SAMA D.10109 (Fig. 6a) (1v)). – Cotton, 1961: 203, fig. 208; Lamprell & Healy, 1998: 168, fig. 471.

Condyllocardia rotunda Laseron, 1953: 39, figs 11, 11a (type locality: Narrabeen Beach, Sydney, New South Wales. 33°42'S, 151°18'E. Pre 1951. coll. C. F. Laseron. Lectotype (here selected) (1v) (Fig. 6b) C090558. Paralectotypes, C388182(5v)). – Iredale & McMichael, 1962: 17; Jansen, 1995: 101, fig. 424; Lamprell & Healy, 1998: 168, 476.

Radiocondyla jacksonensis Laseron, 1953: 42, figs 19, 19a (type locality: off Sow and Pigs Reef, Western Channel, Sydney Harbour, 33°50.3'S 151°16.1'E, 11–16 m, 1948. Lectotype (here selected) (1v) (Fig. 6c) C090559. Many valves of paralectotypes C388183). – Iredale & McMichael, 1962: 17; Lamprell & Healy, 1998: 172, fig. 497.

Other material examined. **Queensland.** Off S end Fraser Is., 25°48'S 153°46'E, 73 m, soft corals, 10 Nov. 1976, C379856. Rainbow Beach, Wide Bay, S of Fraser Is., 25°54'S 153°5'E, 1955, C379271 (2v). ESE of Noosa Heads, 26°34'S 153°40'E, 128 m, 30 March 1969, C379266 (1v). Off Cape Moreton, 27°S 153°35'E, 128–183 m, 1967, C378963 (4v). **New South Wales.** E of Yamba, 29°30'S 153°26.3'E, 53 m, 21 Feb. 1972, C378921 (17v). 12 km E of Cakora Point, S of Yamba, 29°39.8'S 153°26.4'E, 55 m, 22 Feb. 1972, C379850 (19v). N of Coffs Harbour, 30°S 153°23'E, 61 m, 22 Feb. 1972, C379853. Off Laurieton, 31°40'S 152°50.4'E, 20 m, 25 Feb. 1972, C366806 (1v). Off Nelson Bay, Port Stephens, 32°43'S 152°15'E, 46–73 m, 1967, C366812 (18v) and C366814, (37v). Port Stephens, Fingal Bay, 32°45'S 152°10.5'E, beach, 1950, C366796 (5v). *Sydney area:* Off Patonga Beach, 33°33.6'S 151°16.8'E, 1959, C366801 (3v); Pittwater, 33°37' 151°18'E, 1950, C347807 (4v); Narrabeen Beach, 33°42'S 151°18'E, 1951, C366824, (3v) and C90558 (6v); Narrabeen Lake (=Narrabeen Lagoon), 33°42.9'S 151°16.8'E, 1967, C347808 (1v); 33°43'S 151°40'E, 143 m, 5 Dec. 1978, C378922 (2v); Collaroy Beach, 33°43.7'S 151°18'E, shell sand, 1950, C366310 (20+v); 33°45.4'S 151°21.6'E, 40 m, 29 March 1972, C366805 (6v); Manly Beach, 33°48'S 151°17'E, 1950, C366803 (13v) and 1957, C366795, (18v); Middle Harbour, 33°48.1'S 151°14'E, 1913, C35724 (15v); Fairlight, 33°48.2'S 151°16.4'E, 1970, C347814 (12v); off Fairlight Beach, 33°48.2'S 151°16.4', 6–9 m, in shell rubble, 28 Feb. 1981, C366748 (1pr), same locality, 5 m, in shell rubble, 7 May 1982, C405392 (20+pr wet); North Harbour, 33°48.5'S 151°16.5'E, 4 m, with weed, 1950, C347813 (6v) and C347817, (20+v); Little Manly Beach, 33°48.5'S 151°17.2'E, 1950, C366820, (20+v); Little Manly Point, 33°48.6'S 151°17.15'E, 6 m, in rubble and brown algae washings, 1 Dec. 1982 C347810, (52+v dry, 9 pr wet) and 15 m, in rubble, 1 Dec. 1982, C366745 (3pr); Chinamans Beach, 33°48.97'S 151°14.87'E, 1950, C366822 (1v); same locality 4–11 m, 1967, C366802 (11v) and 3.5–7.5 m, 1967, C366826 (10v); Old Mans Hat Point, N Quarantine Station, 33°49.3'S 151°17.4'E, 15 m, 19 June 1884, C366787 (10v); Quarantine Bay, 33°49'S 151°17'E, 27 m, 1950, C347811 (19v) and 9–11 m, 9 March 1969 C366799, (1v); between Grotto and Dobroyd Pts, 275 m off Washaway Beach, 33°49'S 151°16'E, 14.5–18 m, 9 March 1969, C366747 (4v); off Balmoral, 33°49.5'S 151°15.4'E, 3.5–9 m, 1950, C379260 (20+v); between North and South Heads, near North Channel, 33°49.8'S 151°17'E, 9 March 1969, C366823 (1pr); 33°50'S 151°19'E, 46–73 m, 1967, C366779 (12v); 33°50'S 151°18'E, 46 m, associated with sponge, 5 Feb. 1973, C366797 (1pr); Western Channel, 33°50'S 151°16'E, 27 m, 1967, C366798 (15v); Western Channel, off Sow and Pigs Reef, 33°50.3'S 151°16.1'E, 1875, C366776, (5v), 9 Jan. 1879, C366782 (20+v) and 7 m, C378553 (27v); 14 May 1881, C366780 (82v), C366828, (23v), and 9 m, C366818 (15v); 11–14.5 m, 1950, C366817 (46v); 1976, C366794, (40+v); off Georges Head, 33°50.5'S 151°15.7'E, 1900, C366830 (1v); Watsons Bay, 33°50.7'S 151°16.7'E, 1888, C11595 (10v); Watsons Bay, off Green Point, 33°50.5'S 151°16.5'E, 6 m, 23 Feb. 1981, C379268 (4v) and 14.6 m, 1887, C47624 (37v); Nielson Park, Bottle and Glass Rocks, 33°50.94'S 151°16.13'E, 3.5–7.5 m, 1950, C366781 (30v), 9 m, 1878, C366784 (4pr), 11–17 m, 1950, C366811 (2pr); off Morts Dock, Balmain, 33°51.4'S 151°11'E, 7 m, 22 Oct. 1963, C347818 (1v); off E end Shark Is., 33°51.6'S 151°15.4'E, 9 m, 1873, C378554 (1pr) and 22 m, 18 Dec. 1879, C366808 (2pr); 2 km E of Minstral Point, 33°56.7'S 151°16.7'E, 38 m, 19 May 1972, C366792 (1v); 33°58'S 151°29'E, 150 m, 18 June 1962, C366775 (1v); Botany Bay, 1.6 km W of Kurnell, 34°0.3'S 151°11'E, 3.5–5.5 m, 17 May 1946, C378924 (1v); Kurnell, Botany Bay, 34°0.58'S 151°12.38'E, 1950, C366777 (6v); Bate Bay, Cronulla Beach, 34°2.5'S 151°10'E, 28 May 1939, C366827 (3v) and 1967, C366786 (20+v); Port Hacking, Gunnamatta Bay, 34°3.95'S 151°8.55'E, low tide, 1950, C347815 (1v); same locality, SW

end, 34°4.3'S 151°8.7'E, in channel, 1950, C347806 (20+v). Shellharbour, 34°35'S 150°52'E, 1994, C378927 (1pr). Warri Beach, Gerringong, 34°44.3'S 150°50'E, 1950, C366804 (15v). 36 km E of Ulladulla, 35°20.3'S 150°52.3'E, 179 m, 17 March 1972, C378928 (1v). Pebbly Beach, 35°36.8'S 150°19.7'E, 1980, C366833 (1v). Batemans Bay, 35°43'S 150°12'E, shell sand on beach, 1950, C366785 (9v). Broulee, near Moruya, 35°51.5'S 150°10.5'E, 1985, C378918 (10v). Bermagui, Shelly Beach, 36°25'S 150°5'E, 1967, C379852 (40+v). E of Bermagui, 36°27'S 150°19'E, 354–384 m, 22 July 1975, C378920 (2v). 32 km SE of Twofold Bay, 37°26'S 150°15'E, 149 m, 19 June 1962, C366837 (15v). 40 km E of Twofold Bay, 37°27'S 150°17'E, 294–304 m, 19 June 1962, C366815 (2v). **Victoria**. Bass Strait, c. 44 km SE of Cape Everard, 38°15'S 149°12'E, 165–274 m, 9 May 1914, C378964 (3v). 30 km SW of Cape Everard, 38°3.83'S 149°8.83'E, 119 m, brown sandy clay, flat outer shelf, 7 May 1969, C378960 (10v). Sandy Point, Western Port, just N of North Arm, 38°24.3'S 145°14.2'E, 7.5 m, sandy mud and shell, 28 Feb. 1977, C378961 (6v). Point Leo, Western Port, 38°26'S 145°5'E, Aug. 1956, C378962 (1v). S of Warrnambool, 38°43'S 142°29'E, 75 m, 24 June 1962, C378958, (1v). **Tasmania**. Murray Pass, Deal Is., Bass Strait, 39°28'S 147°18'E, 30–50 m, in red algae, 9 May 1974, C378948 (1v). East Cove, Deal Is., Bass Strait, 39°30'S 147°20'E, 6–15 m, 3 May 1974, C378937 (3pr). E of King Is., 40°S 144°38.5'E, 46 m, 30 April 1973, C378943 (2v). N of Three Hummock Is., 40°9.2'S 145°11.6'E, 51 m, 24 April 1973, C378953 (2v). SE of King Is., Bass Strait, 40°10.5'S 144°18.6'E, 51 m, 24 April 1973, C378945 (9v). S of King Is., 40°20'S 144°36.4'E, 55 m, 12 April 1973, C378944 (15v). Off Cape Naturaliste, 40°50.6'S 148°46.5'E, 399 m, silty sand and bryozoa, 26 March 1973, C379263 (3v). Off NE coast, 41°3'S 148°42'E, 125 m, 24 March 1931, C378955 (26v). S of West Point, 41°9.2'S 144°24.2'E, 88 m, 14 April 1973, C378940 (7v). NW of Sandy Cape, 41°9.4'S 144°10.6'E, 132 m, 14 April 1973, C378952, (39v). Bass Strait, Marawah (Green Point), 41°10.82'S 144°52.79'E, 27 Dec. 1996, C378947 (7v). W of Sandy Cape, 41°39.6'S 144°28.7'E, 186 m, 15 April 1973, C378951 (31v). Off Long Point, N of Bicheno, 41°45.5'S 148°31'E, 113 m, 27 March 1973, C378931 (26v). Between Cape Sorell and Sandy Cape, 41°49.5'S 144°46'E, 86 m, 15 April 1973, C379860 (1v). N of Cape Lodi, 41°50'S 148°17.3'E, 33 m, fine-medium sand, 24 March 1973, C379262 (9v). S of Cape Lodi, 42°S 148°18'E, 28 m, sandy, 19 March 1973, C378933 (4v). SE of Cape Lodi, 42°S 148°35.5'E, 148 m, medium coarse sand and bryozoa, 19 March 1973, C378934 (2v). Off Cape Forestier, 42°10'S 148°34.7'E, 205 m, pale grey clayey sand and bryozoa, 19 March 1973, C378932 (10v). Great Oyster Bay, 42°10.2'S 148°6.2'E, 14 m, muddy sand, 18 March 1973, C379264 (3v), and 42°20'S 148°13'E, 45 m, yellow brown sandy mud, 18 March 1973, C378941 (5v). Green Cape, Maria Is., 42°43'S 148°1'E, 5.5 m, 26 March 1970, C379859 (2v). S of Maria Is., 42°51'S 148°20.4'E, 157 m, coarse bryozoan sand, 13 March 1973, C379861 (18v). Derwent Estuary, 42°55'S 147°23.5'E, 1970, C68681 (4pr). SW of Low Rocky Point, 42°58.2'S 145°26.6'E, 84 m, 10 April 1973, C378946 (30v). Off Eaglehawk Neck, 43°S 148°13.6'E, 122 m, coarse bryozoan sand, 13 March 1973, C378936 (3v). Tinderbox Bay, S of Hobart, 43°3'S 147°20'E, 15 m, 1955, C378954 (38v). Wedge Bay, off Nubeena, 43°6'S 147°44'E, 7 m, 1967, C378950 (1v). NE of Cape Pillar, 43°10'S 148°6.7'E, 113 m, medium sand and bryozoa, 13 March 1973, C378930 (3v). W of Port Davey, 43°20.3'S 145°48.2'E, 82 m, 9 April 1973, C379851. Off Port Davey, 43°22.5'S 145°44.5'E, 144 m, 9 April 1973, C379858 (10v). S of D'Entrecasteaux Channel, 43°40.4'S 146°50.4'E, 104 m, 2 April 1973, C378935 (20+v). S of Storm Bay, 43°47'S 147°48.5'E, 212 m, 30 March 1973, C379857 (20v). N of Macquarie Harbour, 44°19.8'S 144°51'E, 170 m, 16 April 1973, C378949 (13v). **South Australia**. Normanville, S of Adelaide, 35°26.8'S 138°18.5'E, 1967, C378965 (2v).

Description

Shell. Maximum length 1.62 mm, maximum height 1.67 mm, equilateral, orthogyrate, opaque, either white, brown or combination of the two. Inflation ratio, 1.11–1.65.

Prodissoconch. Maximum length 380 µm, consisting of prodissoconch I and II. Prodissoconch I with one central indentation, prodissoconch II with slight radial pattern and sharp rim. Anterior and posterior prodissoconch auricles present.

Dissoconch. Lunule and escutcheon short and narrow with commarginal sculpture. Outline oval to triangular, proximal dorsal anterior and posterior slopes strongly convex, distal slopes almost straight. External sculpture of commarginal ribs, fine growth lines and 13–19 strong radial ribs. Inner margin denticulate, with 13–19 denticles. Hinge plate narrow and short. Two sculptured lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) long. Right valve anterior cardinal tooth (CA3) proximally arched, divided into anterior cardinal teeth elements

CA3a,b. Posterior cardinal tooth (CP3) vestigial. Left valve with two anterior cardinal teeth (CA2 and CA4), CA4 dorsally bent into the cardinal teeth elements CA4a,b. Two posterior cardinal teeth (CP2 and CP4) present. Internal ligament 70 μ m long, rounded and in resilium.

Anatomy

Material examined

C405392 (20+ specimens), C347810, (9 specimens).

Description

Mantle edge simple. Mantle margin with one posterior fusion between exhalant and inhalant openings. Inhalant opening (Fig. 7A, 1) extends from anterior end to posterior gill connection to the mantle edge. Exhalant siphon absent or very short, barely protruding beyond shell margin. Anus positioned just below posterior adductor muscle. Ctenidia with inner demibranch only, with about 17 filaments, sloping anteroventrally, length more than half shell length. Labial palps small, positioned at tip of most anterior gill filament, very close to anterior adductor muscle. Adductor muscles isomyarian. Small pedal retractor present anteriodorsally. Foot curved anteriorly, with longitudinal groove, sole. Byssus gland not observed.

Dimensions. See Table 3.

Reproduction

Up to 16 embryos and eggs in suprabranchial cavity. One specimen contained three large embryos and four smaller developing eggs, another contained three large embryos and five developing eggs. Embryos observed in specimens sampled in December (C347810).

Distribution

Southern Queensland, New South Wales, Victoria, Tasmania and South Australia. Shallow subtidal, continental shelf, and slope, 4–399 m (live specimens at 5–6 m depth, other depths shells only). Empty shells have been sorted from rubble, shell rubble, sand, bryozoan sand, clayey sand, clay, mud, sandy mud. Have been found live subtidally in rubble and brown algae washings (C405392, C347810).

Remarks

This taxon, as recognised here, is very variable in both colour and shape. The growth of the shell from juvenile to adult passes through a phase with convex anterior and posterior margins (see Fig. 6c–e) (like the type of *C. notoaustralis*), and a slightly elongated form (note the non-isometric pattern in Fig. 9). The convexity becomes less pronounced as the shell enlarges. The shells from New South Wales are the largest and, around Sydney, brown (like the type of *C. jacksonensis*). However, examination of specimens from throughout the range has failed to establish any character, colour or form that consistently separates these phenotypes. See Table 3 for shell measurements of these two forms.

This species is easily confused with juvenile *C. subradiata* but the smaller auricular prodissoconch (0.31 ± 0.06 mm versus 0.66 ± 0.11 mm ($X \pm SD$)) and the simpler hinge readily separate them.

Condyllocardia notoaustralis may be separated from the closely similar species, *C. pectinata* by the consistently equilateral beaks.

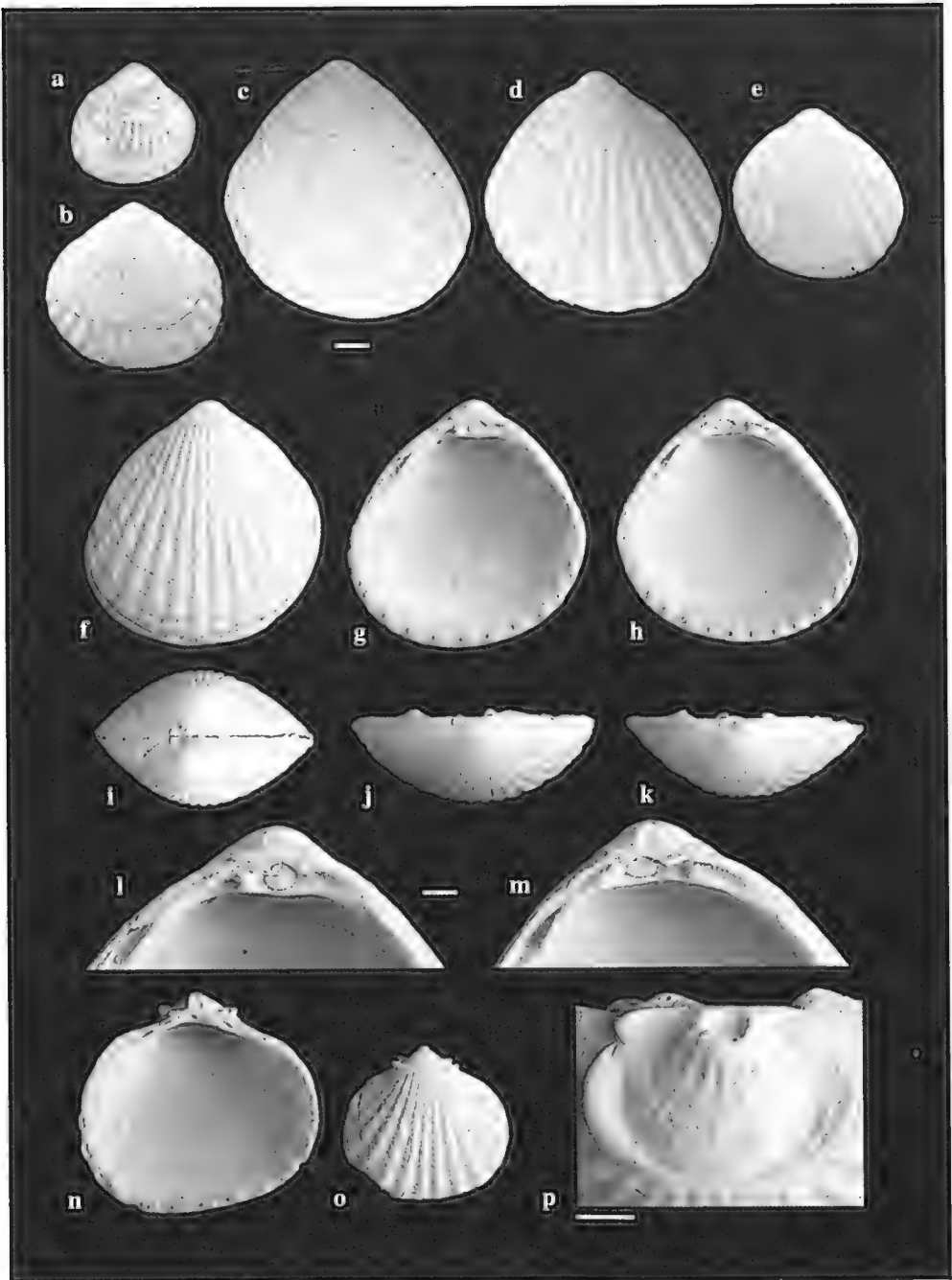


Fig. 6. *Condylocardia notoaustralis*. *a*, *Condylocardia notoaustralis* holotype SAMA D.10109, off Beachport, South Australia. *b*, *Condylocardia rotunda* lectotype C090559 Narrabeen Beach, Sydney, New South Wales. *c*, *Radiocondyla jacksonensis* lectotype C090559, off Sow and Pigs Reef, Sydney Harbour, New South Wales. *d*, *R. jacksonensis* paralectotype no. 3. *e*, *R. jacksonensis* paralectotype no. 4 (*d* and *e* both in lot C388183). *f*–*m*, C379265, off Sow and Pigs Reef, New South Wales. *g*, *j*, *l*, same valve. *h*, *k*, *m*, same valve. *n*–*p*, C379851, W of Port Dovey, Tasmania. Scale bars: *a*–*k*, *n*, *o*, 200 μ m; *l*, *m*, 100 μ m; *p*, 100 μ m.

Table 3. Measurements of specimens of *Condyllocardia notaustralis* Cotton, 1930

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condyllocardia notaustralis</i> , holotype, SAMA D.10109 (Fig. 6a)	0.73	0.80	0.19	0.33	1.11
<i>Condyllocardia rotunda</i> , lectotype, C090558 (Fig. 6b)	1.03	0.97	0.32	0.38	1.36
<i>Radiocondyla jacksonensis</i> , lectotype, C090559 (Fig. 6c)	1.44	1.50	0.25	0.54	1.33
<i>Condyllocardia notaustralis</i> (brown northern phenotype), C366781	1.62	1.67	0.26	0.65	1.25
	1.45	1.47	0.31	0.49	1.48
	1.41	1.35	0.28	0.48	1.47
	1.22	1.09	0.32	0.37	1.65
	1.13	1.08	0.26	0.33	1.71
<i>Condyllocardia notaustralis</i> (white southern phenotype), C378951	1.33	1.26	0.37	0.57	1.17
	1.32	1.33	0.37	0.49	1.35
	1.36	1.34	0.35	0.53	1.28
	1.33	1.12	0.35	0.43	1.55
	1.30	1.18	0.38	0.46	1.41

The holotype of *C. notaustralis* (Fig. 6a) does not match the original illustration well (Cotton 1930: p.238, fig. 13). The illustrated specimen has curved radial ribs, not straight central ribs as in the type specimen, and 12 instead of the 13 radial ribs mentioned in the text. The originally cited size is 1.5 mm × 1.4 mm (probably length × height). This is quite different from the actual measurements, 0.73 mm long, 0.80 mm high. Although the illustration of the type is very imprecise, the factor 2 measuring error may be due to calculation error. Although Cotton in his original description does not refer to a holotype but just 'type', he does list the type with holotype status in 1962: p. 263. Thus, no confusion should exist as to which specimen was measured and illustrated, unless the type has been switched between the description in 1930 and the subsequent reference to it in 1962.

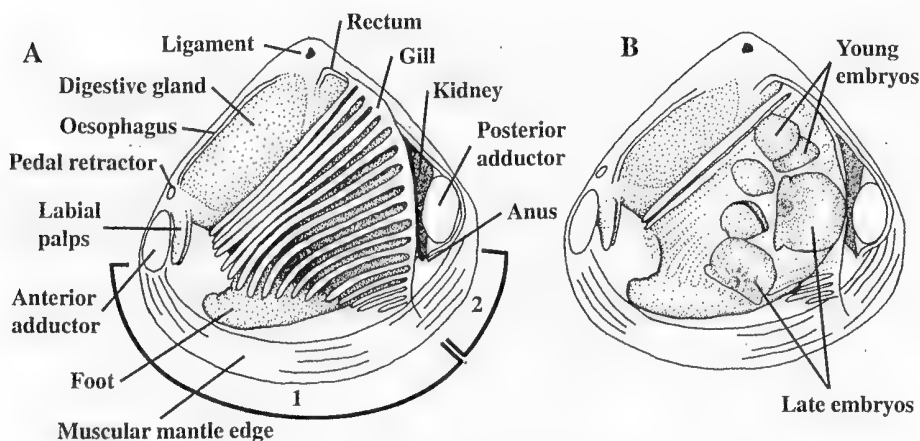


Fig. 7. *Condyllocardia notaustralis*. A, Animal with demibranch intact; 1, is the inhalant opening and 2, the exhalant opening. B, Animal with embryos of varying stages of development in the suprabranchial cavity.

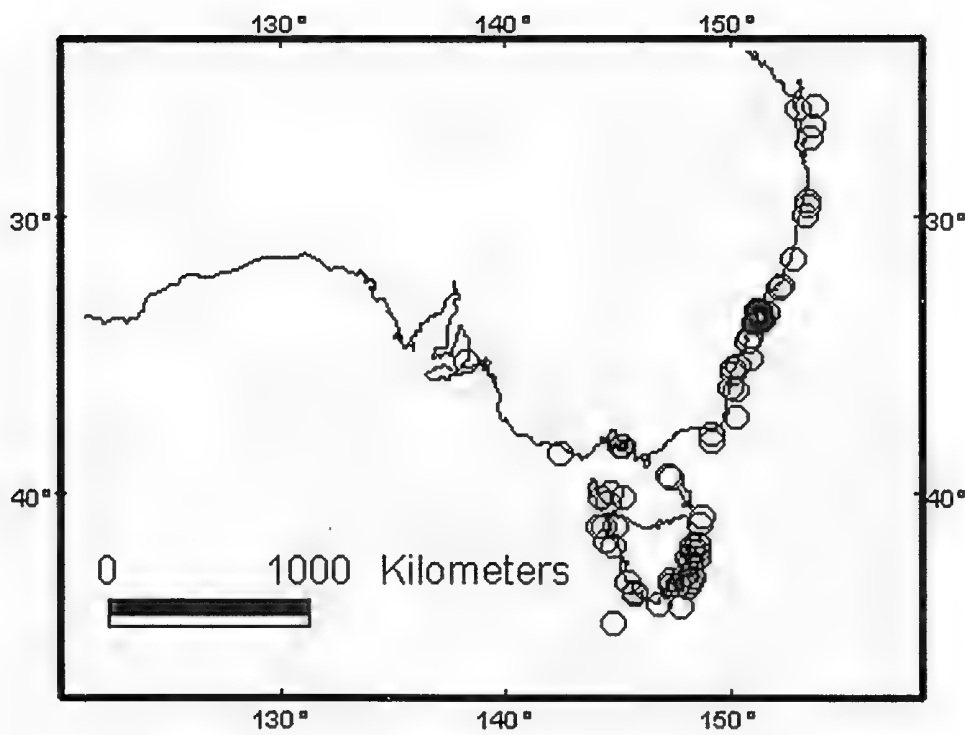


Fig. 8. Distribution of *Condylocardia notoaustralis*.

Condylocardia australis Bernard, 1896 from St Paul Island in the southern Indian Ocean is very similar to the oval, white specimens predominating in southern Australia. It seems unlikely that there has been a genetic exchange between these very isolated populations and

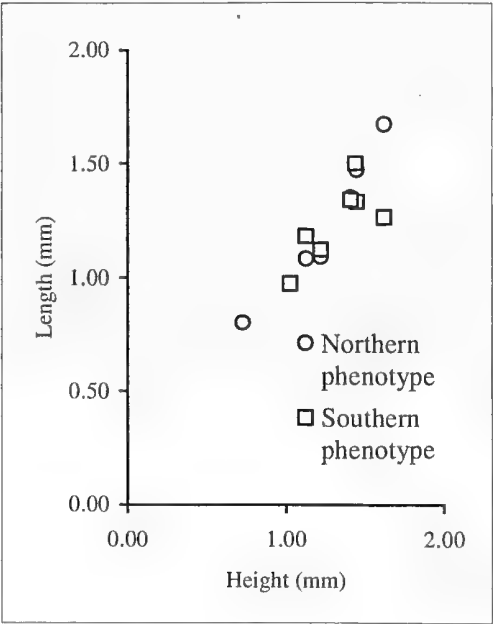


Fig. 9. *Condylocardia notoaustralis*. Height as a function of length in types, one southern and one northern population.

these taxa are maintained as distinct until more is known about *C. australis*. Three records of *C. australis* have been published from Australia (see synonymy). Cotton (1930) treated these records as misidentifications and described the Australian species as *C. notoaustralis*.

Successive stages from eggs to ready-to-hatch embryos have been found brooded in the suprabranchial cavity (Fig. 7B). This indicates either continuous brooding or an extended period in which reproduction takes place.

Condylocardia pectinata (Tate & May, 1900)

(Figs 10a–i, 12)

Carditella pectinata Tate & May, 1900: 103 (type locality: Derwent Estuary, Tasmania. Holotype (Fig. 10a) TMH 7512/E171 (2 valves presumably from same specimen)). – Tate & May, 1901: 435, pl. 27, figs 96, 97.

Condylocardia pectinata (Tate & May, 1900). Hedley, 1902: 318. – Pritchard & Gatliff, 1904: 231; Verco, 1908a: 359; Hedley, 1918: M17, 163; May, 1921: 17, no. 113; May, 1923: pl. 7, fig. 10; Macpherson & Chapple, 1951: 17.

Cuna pectinata (Tate & May, 1900). Hedley & May, 1908: 125, pl. 25, figs 43–45.

Condylocardia acuta Cotton, 1931: 353, fig. 18 (type locality: Cape Borda, South Australia. Holotype (Fig. 10b) SAMA D.10128).

Radiocondyla pectinata (Tate & May, 1900). Allan, 1950: 307, text fig. 11. – Kershaw, 1955: 296; Cotton, 1961: 207, fig. 212. Macpherson & Gabriel, 1962: 321; Lamprell & Healy, 1998: 172, fig. 499.

Radiocondyla acuta (Cotton, 1931). Cotton, 1961: 208, fig. 211. – Lamprell & Healy, 1998: 174, fig. 500.

Other material examined. **New South Wales.** 9–12 km NE of Cape Three Points, 33°32.5'S 151°31.4'E, 75–91 m, sticky mud and shell, 25 Feb. 1898, C16912 (2v). Sydney, Middle Harbour, 33°48.1'S 151°14'E, 1926, C345156 (23v). 26 km E of Wollongong, 34°25'S 151°15'E, 183 m, Aug. 1902, C18229 (20+). Broulee, near Moruya, 35°51.5'S 150°10.5'E, 1985, C380085 (1v). 40 km E of Twofold Bay, 37°27'S 150°17'E, 294–304 m, 19 June 1962, C366838 (2v). **Victoria.** Bass Canyon, 53 km S of Cape Conran, 38°18.33'S 148°39'E, 750 m, May 1969, C380088 (3v). Bass Strait, 44 km S of Marlo, 38°12'S 148°35'E, 146 m, flat outer shelf, 7 May 1969, C380090 (8v). **Tasmania.** Bass Strait, E of Grassy, King Is., 40°11'S 144°39'E, 58 m, 23 June 1962, C380078 (9v). Bass Strait, Marawah (Green Point), 41°10.82'S 144°52.79'E, 27 Dec. 1996, C380087 (2v). Great Oyster Bay, 42°20'S 148°13'E, 45 m, yellow brown sandy mud, 18 March 1973, C380094 (5v). Green Cape, Maria Is., 42°43'S 148°1'E, 5.5 m, sublittoral algae, 26 March 1970, C380092 (3v). Derwent Estuary, 42°55'S 147°23.5'E, 1902, C10737 (7v). Eaglehawk Bay, Eaglehawk Neck, 43°1'S 147°55'E, 27 May 1903, C17718 (3v). Tinderbox Bay, S of Hobart, 43°3'S 147°20'E, 15 m, 1955, C380095 (43v). Wedge Bay, off Nubeena, 43°6'S 147°44'E, 7 m, 1967, C380076 (7v). Off Cape Pillar, 43°13'S 148°5'E, 183 m, 17 Dec. 1907, C29081 (3v). South Bruny Is., Great Taylor Bay, 43°27'S 147°10'E, 8 m, algae on sandy bottom, 14 Feb. 1973, C380093. **Western Australia.** Esperance, 33°52'S 121°54'E, 1968, C380096 (1v). Off Esperance, 34°7.4'S 121°12.7'E, fine sand, Feb. 1981, C380086 (5v) and 70–90 m, fine sand and shell, Feb. 1981, C380081 (1v). Off Albany: 34°54'S 118°50'E, 68 m, sand and broken shell, 21 March, 1980, C380083 (1pr); 35°14.4'S 118°20.5'E, 75 m, sand and shell, 12 March 1980, C380084 (1v); 35°9'S 117°46'E, 62 m, sand, 17 March 1980, C380082 (1v). Kilcarnup, N side of Margaret River, 33°57'S 114°59'E, 1 Jan. 1972, C380091 (1v).

Description

Shell. Maximum length 1.72 mm, maximum height 1.65 mm, inequilateral, orthogyrate, semitransparent and colourless or white to light brown. Inflation ratio, 1.32–1.62.

Prodissoconch. Maximum length 420 µm, consisting of prodissoconch I and II. Prodissoconch I with one central indentation and prodissoconch II with slight radial pattern and sharp rim. Anterior and posterior prodissoconch auricles present.

Dissoconch. Lunule and escutcheon short, narrow with commarginal sculpture. Outline oblique triangular, with extended anterior end and short, sharply angled posterior end. External sculpture of commarginal ribs and 16–17 strong radial ribs. Inner margin

denticulate, with 16–17 denticles. Hinge plate narrow and short. Two sculptured lateral teeth present in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) long. Right valve anterior cardinal tooth (CA3) ventrally arched, subdivided into anterior cardinal elements CA3a,b. Slender ventrally directed posterior cardinal tooth (CP3) present and divided into cardinal elements CP3a,b. Left valve anterior cardinal teeth (CA2 and CA4) present, CA4 divided into CA4a,b. Posterior cardinals (CP2 and CP4) present, CP4 vestigial. Internal ligament 120 μm long, rounded, in resilium.

Dimensions. See Table 4.

Distribution

Central New South Wales, south to southwestern Western Australia and Tasmania. Subtidal, down to continental slope, from 6 to 750 m depth. Shells found in mud, sand, shell sand or on algae in the subtidal zone. This species is only known from shells.

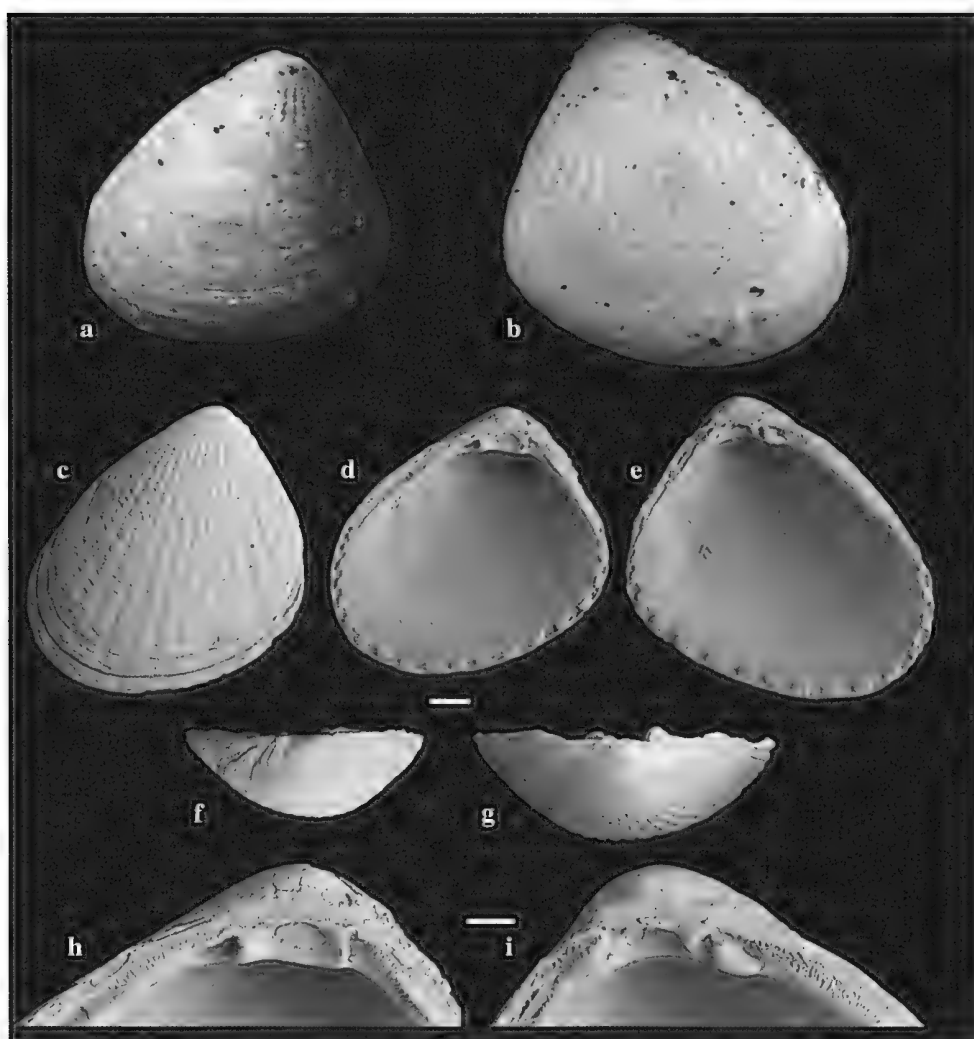


Fig. 10. *Condylocardia pectinata*. *a*, *Carditella pectinata* holotype TMH 7512/E171, Derwent Estuary, Tasmania. *b*, *Condylocardia acuta* holotype SAMA D.10128, Cape Borda, South Australia. *c–i*, C380076, Wedge Bay, Tasmania. Scale bars: *a–g*, 200 μm ; *h, i*, 100 μm .

Table 4. Measurements of specimens of *Condylocardia pectinata* (Tate & May, 1900)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condylocardia pectinata</i> , holotype (data from original description), TMH 7512/E171 (Fig. 10a)	1.50	1.50	-	-	-
<i>Condylocardia acuta</i> , holotype, SAMA D.10128 (Fig. 10b)	1.72	1.65	0.37	0.65	1.32
<i>Condylocardia pectinata</i> , C.380076	1.39	1.33	0.33	0.51	1.36
	1.62	1.53	0.37	0.51	1.59
	1.26	1.22	0.42	0.39	1.62
	1.39	1.29	0.39	0.43	1.62
	1.32	1.31	0.33	0.43	1.53

Remarks

This species is consistent in shape and sculpture and readily identifiable. Cotton (1931) distinguished *C. acuta* because it had fewer radial ribs than *C. pectinata*. However, this can hardly be valid as *C. acuta* has '18 ribs' and *C. pectinata* has '15 or more ribs' according to the original descriptions. Both radial rib numbers are within the range of the phenotypic variation of the species as interpreted herein (see description).

Condylocardia pectinata is most similar to *C. notoaustralis*, from which it can be separated by the inequilateral shell.

There appear to be large gaps in the distribution of *C. pectinata*, especially in South Australia and eastern Western Australia. It is unclear whether the gaps are due to the lack of sampling effort in these areas, true absence due to lack of suitable habitat, the existence of genuinely disjunct populations or cryptic species.

Condylocardia rectangularis Cotton, 1930

(Figs 11a–k, 12)

Condylocardia porrecta Hedley, 1906b. Hedley & May, 1908: 125, pl. 25, figs 41, 42 (not Hedley, 1906b).

Condylocardia rectangularis Cotton, 1930: 237, fig. 10 (type locality: off Beachport, South Australia, 73 m. Holotype SAMA D.14979 (ex. D.10113) (it is questionable whether the two valves belong to the same individual, see Table 5) (left valve illustrated Fig. 11a)). – Cotton, 1961: 203, fig. 205; Lamprell & Healy, 1998: 168, fig. 473.

Radiocondyla arizela Iredale, 1936: 272 (type locality: off Cape Pillar, Tasmania, 43°13'S 148°5'E, 183 m, 17 Dec. 1907. coll. and pres. C. Hedley and W. L. May. Lectotype (here selected) (1v) (Fig. 11b) C029082; Paralectotypes C388186, (Fig. 11e–k) (4v)). – Kershaw, 1955: 296 (sic *arezela*); Iredale & McMichael, 1962: 17; Lamprell & Healy, 1998: 172.

Other material examined. **Tasmania.** S of D'Entrecasteaux Channel, 40°39.5'S 147°20.5'E, 95 m, 1 April 1973, C379880 (31v) and 43°40.4'S 146°50.4'E, 104 m, 2 April 1973, C379883 (20+v). Off Cape Naturaliste, 40°50.6'S 148°46.5'E, 399 m, silty sand and bryozoa, 26 March 1973, C379885 (1v). SE of Cape Lodi, 42°S 148°35.5'E, 148 m, medium coarse sand and bryozoa, 19 March 1973, C379888 (1v). W of Port Davey, 43°20.3'S 145°48.2'E, 82 m, 9 April 1973, C379886 (4v). 3 km S Tasman Head, S Bruny Is., 43°33.75'S 147°19.35'E, 73 m, 24 March 1970, C379882 (16v). S of South East Cape, 43°42.2'S 146°18.6'E, 108 m, 4 April 1973, C379881 (14v). SE of Macquarie Harbour, 42°30'S 145°1'E, 104 m, 11 April 1973, C379889 (1v). SW of Sandy Cape, 41°39.5'S 144°37.1'E, 130 m, 15 April 1973, C379887 (6v). S of West Point, 41°9.2'S 144°24.2'E, 88 m, 14 April 1973, C379884 (4v). **South Australia.** SE of Kangaroo Is., 37°10'S 138°30'E, 155 m, 26 June 1962, C379879 (1v).

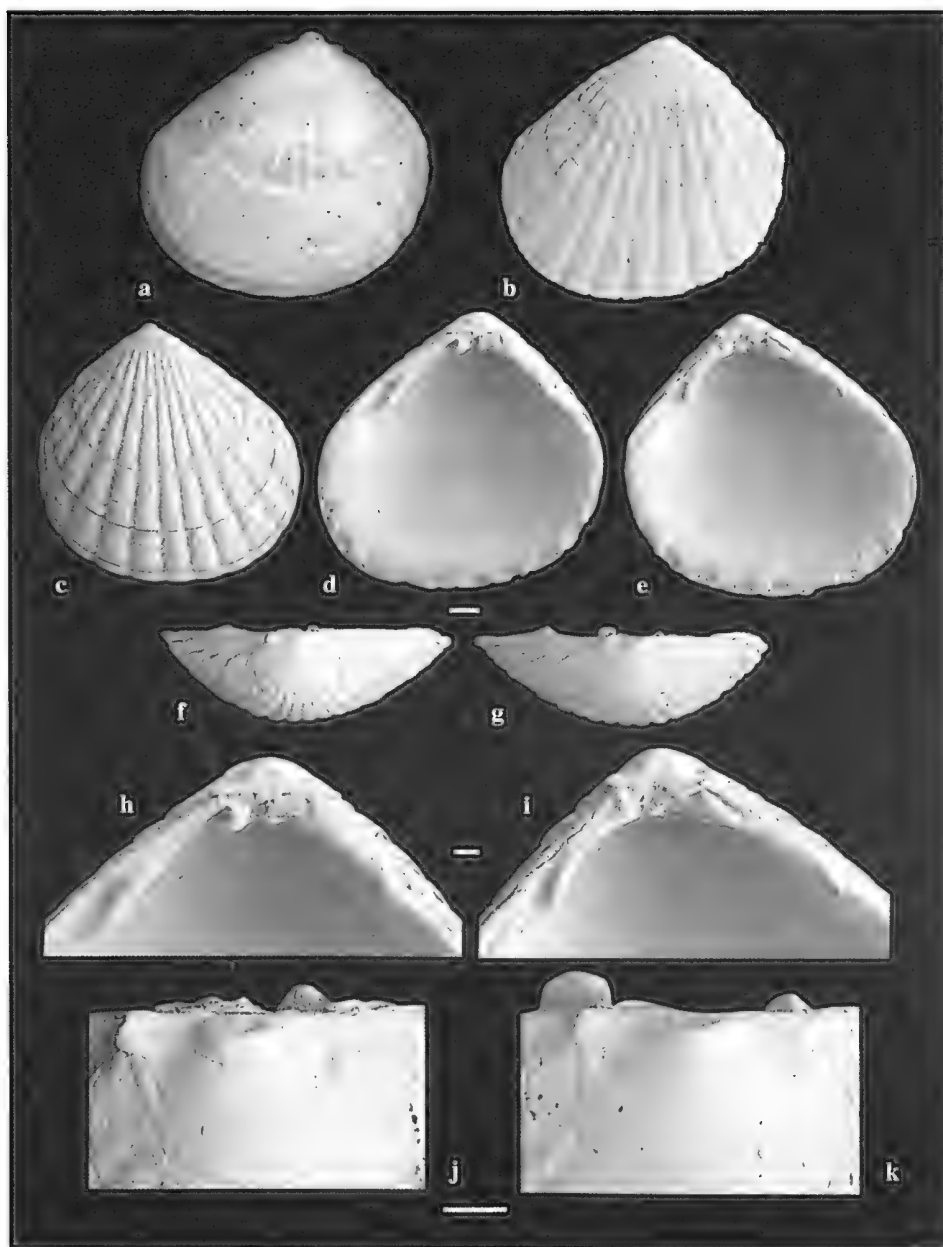


Fig. 11. *Condylocardia rectangularis*. *a*, *Condylocardia rectangularis* holotype SAMA D.14979, off Beachport, South Australia. *b*, *Radiocondyla arizela* lectotype C029082, off Cape Pillar, Tasmania. *c–k*, *Radiocondyla arizela* paralectotypes C388186, off Cape Pillar, Tasmania. Scale bars: *a–g*, 200 µm; *h, i, j, k*, 100 µm.

Description

Shell. Maximum length 2.21 mm, height 1.99 mm, slightly inequilateral, orthogyrate, translucent, white or light brown. Inflation ratio, 1.38–1.75.

Prodissoconch. Maximum length 480 μ m, consisting of prodissoconch I and II. Prodissoconch I with one central indentation, prodissoconch II with slight radial pattern and sharp rim. Anterior and posterior prodissoconch auricles present.

Dissoconch. Lunule and escutcheon short, narrow, with commarginal sculpture. Outline triangular with anterior end slightly longer than posterior end. External sculpture of few major commarginal ribs, numerous commarginal growth lines and 13–14 flat but strong radial ribs. Inner margin denticulate with 13–14 denticles. Hinge plate narrow and short. Two sculptured lateral teeth in each valve. Lateral teeth of medium length (about half length of dorsal slopes), consisting of anterior LAI and posterior LPIII in right valve and anterior LAII and LPII in left valve. Right valve anterior cardinal tooth (CA3) strongly curved proximally, divided into anterior cardinal elements CA3a,b. Posterior cardinal CP3 visible, divided into CP3a,b. Left valve anterior cardinal teeth (CA2 and CA4) present, CA4 divided into CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP2 the largest. Internal ligament 120 μ m long, rounded, in resilium.

Dimensions. See Table 5.

Distribution

Tasmania and South Australia, from 9–399 m. Found in silty sand and sand with bryozoans. This species is only known from shells.

Table 5. Measurements of specimens of *Condylocardia rectangularis* Cotton, 1930

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI \times 2
<i>Condylocardia rectangularis</i> , holotype, SAMA D.14979 Left valve	2.21	1.96	0.48	0.63	1.75
Right valve, (Fig. 11a)	2.06	1.84	0.53	0.64	1.61
<i>Radicondyla arizela</i> , lectotype, C029082 (Fig. 11b)	1.92	1.78	0.39	0.60	1.60
<i>Condylocardia rectangularis</i> , C379881	2.13	1.99	0.31	0.71	1.50
	1.69	1.91	0.35	0.52	1.63
	1.66	1.76	0.39	0.60	1.38
	1.78	1.93	0.40	0.62	1.44
	1.57	1.67	0.45	0.47	1.67

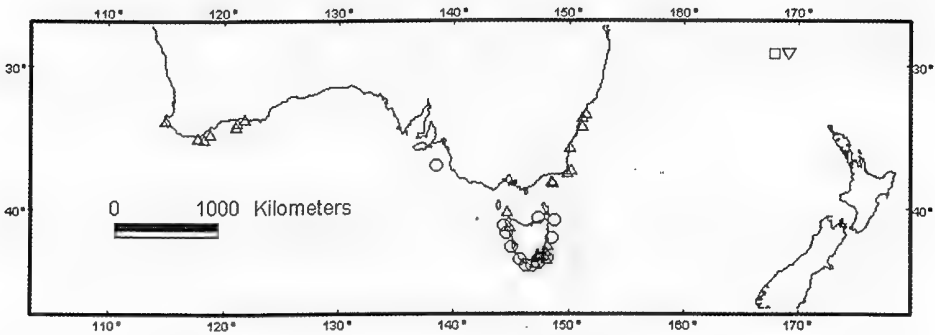


Fig. 12. Distribution of *Condylocardia rectangularis* (O), *C. pectinata* (Δ), *C. annieae* n. sp. (∇) and *Condylocuna jimbecki* (□).

Remarks

This species is very distinct, with wide, flat radiating ribs, inequilateral beaks and strongly hooked CA3. The prodissoconch readily separates *C. rectangularis* from *Cunanax subradiata*, the former having anterior and posterior prodissoconch auricles. It can be separated from *Condylocardia notoaustralis* by its flat, wide ribs, sharp anterior and posterior slopes and larger size and from *Condylocardia pectinata* by its narrow radiating ribs. *Condylocardia limaeformis* has fewer radials (up to 12 versus 13–14 in *C. rectangularis*).

Iredale (1936) renamed a shell, figured by Hedley and May (1908, pl. 25, figs 41, 42, as *Condylocardia porrecta*), *Radiocondyla arizela*, apparently unaware of Cotton's earlier description of the same taxon from South Australia. He also made it the type species of *Radiocondyla* Iredale, 1936. Despite being easily separable from the other members of *Condylocardia* revised herein, the taxon has no characters that would merit separation at the generic level (see also Remarks for the genus *Condylocardia*).

The disjunct distribution is possibly due to inadequate sampling in Victoria and South Australia.

Genus *Austrocardiella* n. gen.

Type species: *Condylocardia isosceles* Cotton, 1930.

Diagnosis

Very small condylocardiine, less than 1.5 mm long. Prodissoconch >40% length of adult, with commarginal pattern. Prodissoconch with single central or three radial indentations. Right valve anterior cardinal teeth consist of CA3 and CA5. Shell ovate, with weak commarginal ribs. Ventral margin smooth.

Remarks

One member of this group has been included in various genera (*Condylocardia*, *Condylocuna* and *Benthocardiella*) reflecting the non-typical morphology of the shell. The lack of radial ribs on the dissoconch separates *Austrocardiella* from *Condylocardia*, while the sculptured prodossoconch distinguishes the genus from *Benthocardiella*. *Austrocardiella* can be distinguished from *Condylocuna* by the additional anterior cardinal hinge tooth CA5 (see Fig. 31) set on a large broad hinge plate and the weaker external commarginal sculpture.

The presence of one species in this group with a closely similar prodossoconch to species of *Condylocuna* suggests a close relationship between the two genera.

Etymology

Austro derived from Australia, *cardiella* meaning 'little heart'.

Austrocardiella isosceles (Cotton, 1930)

(Figs 13a–g, 16)

Condylocardia trifoliata Hedley, 1906b. Verco, 1907: 109. – Verco, 1908a: 359 (not of Hedley, 1906b).

Condylocardia isosceles Cotton, 1930: 238, fig. 11 (type locality: Backstairs Passage, South Australia).

Holotype (Fig. 13a) SAMA D.10108.

Condylocuna isosceles (Cotton, 1930). Laseyron, 1953: 40. – Cotton, 1961: 206, fig. 207.

Benthocardiella isosceles (Cotton, 1930). Lamprell & Healy, 1998: 170, fig. 480.

Other material examined. **South Australia.** Off South Australian coast, deep water, 1907, C25988 (6v). **Western Australia.** Off Esperance, 34°2.75'S 121°0.6'E, coarse shell sand, 3 Feb. 1981, C382249 (2v). Off Albany: 34°44.9'S 118°50.5'E, 70 m, sand and shell, 21 March 1980, C382247 (1v); 35°6'S



Fig. 13. *Austrocardiella isosceles*. a, *Condyllocardia isosceles* holotype SAMA D.10108, Backstairs Passage, South Australia. b–g, C382307, off Albany, Western Australia. Scale bars: a–e, 200 µm; f, g, 100 µm.

118°39'E, 76 m, sand and broken shell, 20 March 1980, C382307 (13v); 35°8.5'S 118°20'E, 75 m, sand, 12 March 1980, C382245 (9v); 35°19'S 118°3.4'E, 80 m, fine sand and shell, 12 March 1980, C382244 (2prs). W of Green Head, 30°1'S 114°45'E, 52 m, Feb. 1982, C382248 (1v).

Description

Shell. Maximum length 0.97 mm, maximum height 1.1 mm, equilateral, orthogyrate, translucent or opaque white. Inflation ratio 1.10–1.27.

Prodissoconch. Maximum length 460 µm, consisting of prodissoconch I and II. Prodissoconch I with one central indentation, prodissoconch II with about ten commarginal ribs and thickened rim.

Dissoconch. Lunule and escutcheon absent. Outline oval, with anterior end slightly extended and broadly rounded, posterior end weakly angled. External sculpture of many weak rounded commarginal ribs. Inner margin smooth. Periostracum thin and smooth. Hinge plate wide. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half length of dorsal slopes. Right valve anterior cardinal teeth (CA3 and CA5) present, cardinal tooth CA3 most prominent, cardinal CA5 vestigial. Posterior cardinal tooth (CP3) arched, divided into CP3a,b. Left valve anterior cardinal tooth (CA4) arched, divided into cardinal elements CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP4 very small. Internal ligament 75 µm long, rounded, in resilium.

Dimensions. See Table 6.

Distribution

Backstairs Passage, South Australia and from off Esperance to off Green Island, Western Australia, 52–80 m depth. Found in fine to coarse sand and shell sand. This species is only known from shells.

Remarks

Austrocardiella isosceles can be readily separated from *A. pouli* n. sp. by the number of commarginal ribs on the prodissoconch (*A. isosceles* about ten, *A. pouli* about six). Using

Table 6. Measurements of specimens of *Austrocardiella isosceles* (Cotton, 1930)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condylocardia isosceles</i> , holotype, SAMA D.10108 (Fig. 13a)	0.94	1.02	0.45	0.37	1.27
<i>Austrocardiella isosceles</i> , C025988	0.97	1.00	0.45	0.42	1.15
	0.91	1.04	0.46	0.40	1.14
	0.93	1.05	0.46	0.41	1.13
	0.95	1.08	0.43	0.43	1.10
	0.94	1.10	0.44	0.46	1.02

SEM, other characters such as the features of the hinge can also be used to separate the taxa in this genus. *Austrocardiella isosceles* can be separated from *A. trifoliata* by the absence of three radiating indentations on prodissococonch I.

The large gap in distribution in the Great Australian Bight is probably due to the lack of adequate sampling in that area.

Austrocardiella pouli n. sp.

(Figs 14a–i, 19)

Material examined

Holotype. (Fig. 14a, h, i). WAM S12719, off Albany, 35°6'S 118°39'E, 76 m, sand and broken shell, 20 March 1980, coll. HMAS Moresby.

Paratypes. C381978, (25v, Fig. 14b–g), C382308, (27v), off Albany, 35°6'S 118°39'E, 76 m, sand and broken shell, 20 March 1980, coll. HMAS Moresby; WAM S12720 (5v), off Albany, 35°14.8'S 118°30'E, 124 m, sand, 20 March 1980, coll. HMAS Moresby.

Other material examined. **Western Australia.** Great Australian Bight, 33°5'S 128°40'E, 75 m, 5 July 1962, C381993 (6v). *Off Esperance:* 34°12.85' 121°6'E, 75 m, coarse sand and shell, Feb. 1981, C381990 (1v), 34°2'S 121°12.5'E, 76 m, coarse sand and shell, Feb. 1981, C381961 (5v), 34°21.6'S 121°9.6'E, 70–90 m, fine sand and shell, Feb. 1981, C381989 (1v), 34°11.2'S 121°7.7'E, sand, Feb. 1981, C381992 (1v), 34°22.9'S 121°3.5'E, 85 m, coarse shell sand, Feb. 1981 C381991 (8v). *Off Albany:* 34°44.9'S 118°50.5'E, 70 m, sand and shell, 21 March 1980; C381983 (1pr), 34°57'S 119°E, 73 m, sand and weed, 21 March 1980 C381977 (2v); 35°2.4'S 118°50'E, 73 m, sand and broken shell, 21 March 1980, C382246 (31v); 35°14.4'S 118°20.5'E, 75 m, sand and shell, 12 March 1980, C381975 (20+v); 35°8.5'S 118°20'E, 75 m, sand, 12 March 1980, C381972 (9v); 35°18'S 118°15'E, 62 m, 1930, C382252 (3v); 35°6.4'S 118°10.6'E, 72 m, fine sand, 12 March 1980, C381970 (1v); 35°14.7'S 118°10.4'E, 71 m, 12 March 1980, C381969 (1v); 35°19'S 118°3.4'E, 80 m, fine sand and shell, 12 March 1980, C381967 (20+v); 35°24.4'S 118°2.8'E, 150 m, sand, 12 March 1980, C381966 (21v); 35°10'S 117°52.7'E, 57 m, sand, 13 March 1980, C381974 (8v); 35°9.1'S 117°49'E, 64 m, coarse sand, 13 March 1980, C381973 (7v); 35°9'S 117°46'E, 62 m, sand, 17 March 1980, C381981 (1v). *Off Rottnest Island:* 31°43.1'S 115°15'E, 100 m, broken shell and coral, Jan. 1981, C381964 (1v); 31°41.1'S 115°14'E, 98 m, broken shell and coral, Jan. 1981, C381997 (4v); Direction Bank, 31°45'S 115°16.4'E, 93 m, 12 Nov. 1980, C381988 (18v); Direction Bank, Stn 62, 31°43.4'S 115°13.8'E, 120 m, 12 Nov. 1980, C381984 (1v) and C381985 (5v); Direction Bank, 31°42.2'S 115°13.6'E, 105 m, 12 Nov. 1980, C381986 (7v); 31°37.8'S 115°10.7'E, 110 m, fine sand and broken shell, Jan. 1981, C381996 (20+v). SW of Mandurah, 32°41'S 114°51'E, 146–150 m, 17 March 1972, C381995 (2v). 24 km SW Dongara, 29°20'S 114°43'E, 40 m, 16 Feb. 1976, C381980 (2v). W of Green Head, 30°4.8'S 114°37.7'E, sand and broken shell, Feb. 1982, C381994 (1v). W of Cliff Head, 29°33.8'S 114°17'E, 137 m, 18 Feb. 1976, C381963 (1v).

Description

Shell. Maximum length 0.86 mm, maximum height 1.01 mm, equilateral, orthogyrate, translucent or opaque white. Inflation ratio, 1.16–1.31.

Prodissoconch. Maximum length 420 μm , consisting of prodissoconch I and II. Prodossoconch I with one central indentation, prodossoconch II with six commarginal ribs and thickened rim.

Dissoconch. Lunule and escutcheon absent. Outline oval or slightly triangular, with anterior end slightly extended and broadly rounded, posterior end weakly arched. External sculpture of up to 16 rounded commarginal ribs. Inner margin smooth. Hinge plate narrow centrally. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth

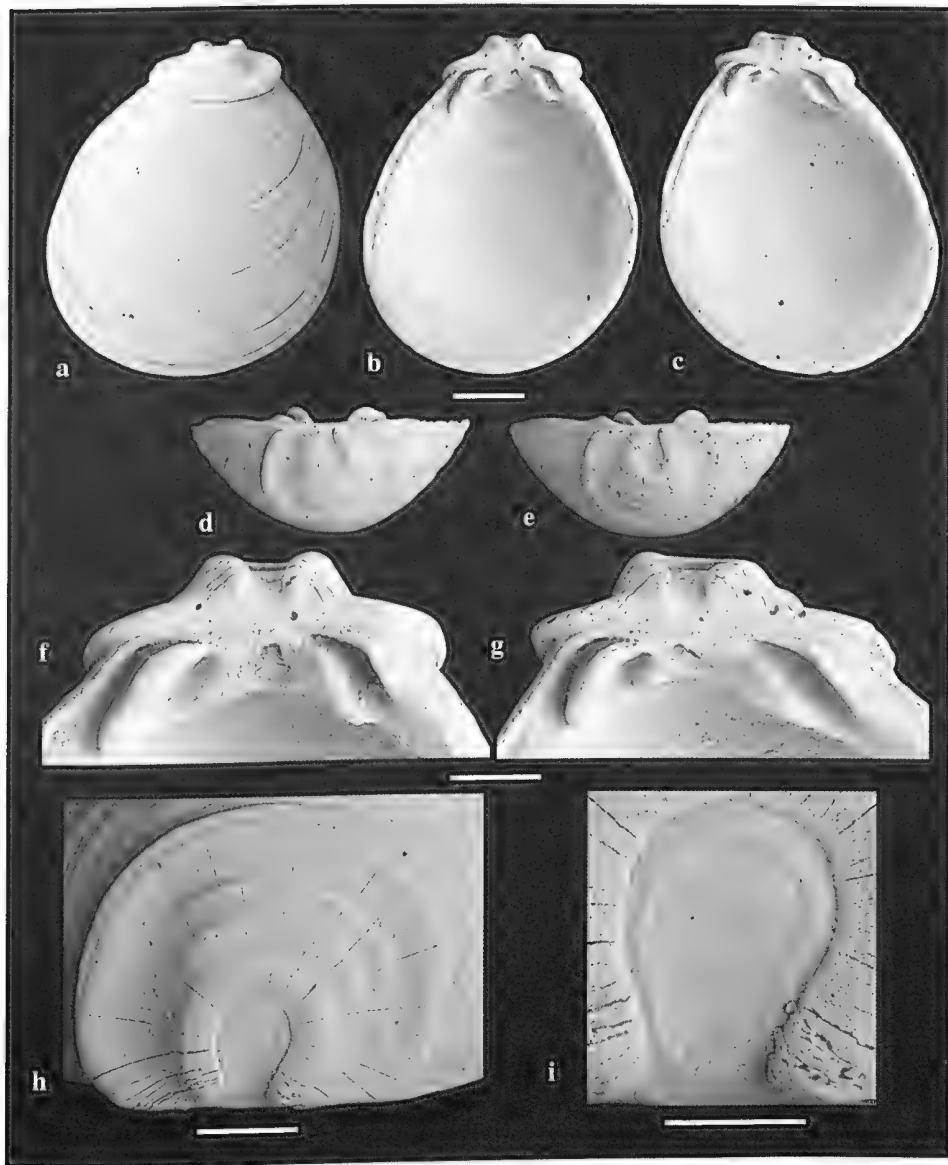


Fig. 14. *Austrocardiella pouli* n. sp. a, h, i, Holotype WAM S12719, off Albany, Western Australia. b–g, Paratypes C381978, off Albany, Western Australia. b, d, f and c, e, g same valves. Scale bars: a–e, 200 μm ; f, g and h, 100 μm ; i, 50 μm .

Table 7. Measurements of specimens of *Austrocardiella pouli* n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Austrocardiella pouli</i> , holotype, WAM S12719 (Fig. 14a, h, i)	0.81	0.92	0.37	-	-
<i>Austrocardiella pouli</i> , paratypes, C382308	0.75	0.90	0.39	0.31	1.21
	0.84	0.96	0.42	0.32	1.31
	0.80	1.01	0.35	0.34	1.18
	0.78	0.93	0.42	0.33	1.18
	0.86	1.01	0.39	0.37	1.16

(LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half length of dorsal slopes. Right valve anterior cardinal teeth (CA3 and CA5) dorsally connected, CA5 about half size of CA3. Posterior cardinal tooth (CP3) arched, divided into two oblique cardinal elements (CP3a,b). Left valve anterior cardinal tooth (CA4) arched, divided into oblique cardinal elements (CA4a,b). Posterior cardinal teeth (CP2 and CP4) dorsally connected and cardinal tooth CP2 about twice size of cardinal tooth CP4. Internal ligament, 57 µm long, triangular, in resilium.

Dimensions. See Table 7.

Distribution

From the middle of the Great Australian Bight to west of Cliff Head, Western Australia, 40–150 m depth. Found in fine to coarse shell and calcareous sand derived from coral. This species is only known from shells.

Remarks

This species is endemic to the continental shelf off S–SW Western Australia, where it coexists with *A. isosceles*. *Austrocardiella pouli* may be readily separated from *A. isosceles* by the six commarginal ribs on the prodissococonch (see Remarks under *A. isosceles*). The single indentation on the prodissococonch separates it from *A. trifoliata*, which has three radiating indentations.

Etymology

Named in memory of the author's father, Poul Middelfart (1941–1998), always supportive and compassionate.

Austrocardiella trifoliata (Hedley, 1906b).

(Figs 15a–l, 16)

Condylocardia trifoliata Hedley, 1906b: 475, pl. 37, figs 20–23 (type locality: Masthead Is., Capricorn Group, Great Barrier Reef, Queensland, 23°32'S 151°45'E, 31–37 m, 25 Oct. 1904. Lectotype (here selected) (Fig. 15a, b) C019393 (1pr), paralectotypes C170779 (20+v, 1pr), paralectotypes in the Tomlin Collection, Department of Zoology, National Museum of Wales, Britain (Oliver, 1982), paralectotypes USNM 201429, (3pr), paralectotypes ANSP 94822, (3v, 4pr)). – Hedley, 1918: M17; Verco, 1907: 109, Verco, 1908b: 18.

Condylocuna trifoliata (Hedley, 1906b). Iredale, 1936: 272. – Lamprell & Healy, 1998: 170, fig. 485.

Condylocuna cambrica Iredale, 1936: 272. – Laserson, 1953: 41, fig. 13, 13a (type locality: Chinamans Beach, Middle Harbour, Sydney, New South Wales, 33°48.97'S, 151°14.87'E, pre 1906, pres. Ms.

L. Parkes, 1906. Lectotype (here selected) (Fig. 15c) C25120, (1v), paralectotypes C388177 (1v) (type material consisted of three valves of *Benthocardiella burtonae* n. sp. (now C388173), not illustrated or mentioned in original description, and two valves of *A. trifoliata*); Iredale & McMichael, 1962: 17; Lamprell & Healy, 1998: 170, fig. 486 (not 484).

Benthocardiella vitrea Laseyron, 1953: 41, figs 15a, b (type locality: Narrabeen Beach, Sydney, New South Wales. 33°42'S, 151°18'E, pre 1951, coll. C. F. Laseyron. Lectotype (here selected) (Fig. 15d) C090566 (1v). Paralectotypes C388226 (1v) (original syntype lot contained specimens of two species, viz., two valves of *A. trifoliata* (here lectotype and paralectotype) and one valve of *Mysella ovata* now C388228 (juvenile, see excluded taxa below))). – Iredale & McMichael, 1962: 18; Lamprell & Healy, 1998: 168, fig. 479.

Other material examined. **Queensland.** NE of Rockhampton, 22°50'S 151°39'E, 64 m, 25 Sep. 1970, C381942 (47v). Great Barrier Reef, near Heron Is., 23°23.5'S 151°56.5'E, 40 m, 3 Oct. 1970, C381946 (1v). Noosa Heads, 26°23'S 153°6'E, 1963, C381950 (1v). NE of Cape Moreton light, 26°55.5'S 153°33.5'E, 115–119 m, 1968, C381948 (9v). **New South Wales.** Off Point Halliday, 32°4.5'S 152°33'E, 15–18 m, 1959, C367548 (1v). Off Crowdy Head, 32°38.15'S 153°0.13'E, 91 m, 16 Dec. 1957, C366875 (14v). Off Nelson Bay, Port Stephens, 32°43'S 152°15'E, 46–78 m, 1967, C366864 (3v). *Sydney area:* Patonga, Broken Bay, 33°33'S 151°16'E, 1960, C366877 (1pr) and 13 Aug. 1971, C366880 (4v); off Patonga Beach, 33°33.6'S 151°16.8'E, 1959, C366862 (8v); Narrabeen Beach, 33°42'S 151°18'E, 1951, C90566 (3v); 33°45.4'S 151°21.6'E, 40 m, 29 March 1972, C366866 (1v); Manly Beach, 33°48'S 151°17'E, 1950, C381951 (1pr), C366876 (1v), C381954 (1v); Chinamans Beach, 33°48.97'S 151°14.87'E, 1906, C25120 (2v), 4–11 m, 1967, C366865 (10v) and 3.5–7.5 m, 1967, C366868, (20+v); between Grotto and Dobroyd Pts, 275 m off Washaway Beach, 33°49'S 151°16'E, 14.5–18 m, 9 March 1969, C366863 (20+v); Quarantine Bay, 33°49'S 151°17'E, 27 m, 1950, C366878 (14v); off Balmoral, 33°49.5'S 151°15.4'E, 3.5–9 m, 1950, C381953 (17v); Balmoral Beach, 33°49.7'S 151°15.03'E, 1957, C366870 (1pr). Western Channel, off Sow and Pigs Reef: 9 Jan. 1879, C366859 (19pr); 9 m, 9 Jan. 1879, C366861 (15v); 7 m, 9 Jan. 1879, C381622 (4pr); 14 May 1881, C366881 (3pr); 7 m, 14 May 1881, C381623 (1pr); 33°50.3'S 151°16.1'E, 11–16 m, 1948, C315613 (17v); 30 Sep. 1976, C366860 (9v). Little Coogee Bay, 33°55.3'S 151°15.6'E, 19 July 1895, C366874 (1pr). **Tasmania.** S of D'Entrecasteaux Channel, 43°40.4'S 146°50.4'E, 104 m, 2 April 1973, C381955 (3v). E of King Is., 40°S 144°38.5'E, 46 m, 30 April 1973, C381957 (1pr). W of West Point, 41°S 144°7.5'E, 104 m, 14 April 1973, C381958 (1v). **South Australia.** Petrel Bay, N of St Francis Is., 32°29'S 133°18'E, 20–30 m, 28 Dec. 1973, C381959 (1v).

Description

Shell. Maximum length 1.46 mm, maximum height 1.29 mm, equilateral, orthogyrate, translucent or opaque white. Inflation ratio, 1.11–1.59.

Prodissoconch. Maximum length 460 µm, consisting of prodissoconch I and II. Prodissoconch I with three radiating indentations, prodissoconch II with three free commarginal ribs and thickened rim.

Dissoconch. Lunule and escutcheon absent. Outline triangular, with anterior end mostly more extended than posterior end. External sculpture of up to 17 commarginal ribs. Inner margin smooth. Hinge plate present. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half length of dorsal slopes. Right valve anterior cardinal teeth (CA3 and CA5) present, CA3 prominent and CA5 vestigial. Posterior cardinal tooth (CP3) strongly dorsally arched, divided into cardinal elements CP3a,b. Left valve anterior cardinal tooth (CA4) arched, divided into cardinal elements CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP2 largest. Internal ligament 88 µm long, rounded, in resilium.

Dimensions. See Table 8.

Reproduction

A single embryo was observed in one dried specimen (C366859, Fig. 15h).

Distribution

From northeast of Rockhampton, Queensland south to Sydney, south and northeast Tasmania and off St Francis Island, South Australia, 4–119 m depth. Habitat unknown. This species is only known from shells.

Remarks

Austrocardiella trifoliata can be separated from *A. pouli* and *A. isosceles* by the three radiating indentations on the prodissoconch, as also seen in all species of *Condyllocuna*.

Iredale (1936) erected *Condyllocuna cambrica* based on the supposed difference in the shape of the northern and southern specimens. However, no significant and consistent difference in shape was found by examining the lectotype using SEM, and the type material is entirely comprised of small specimens.

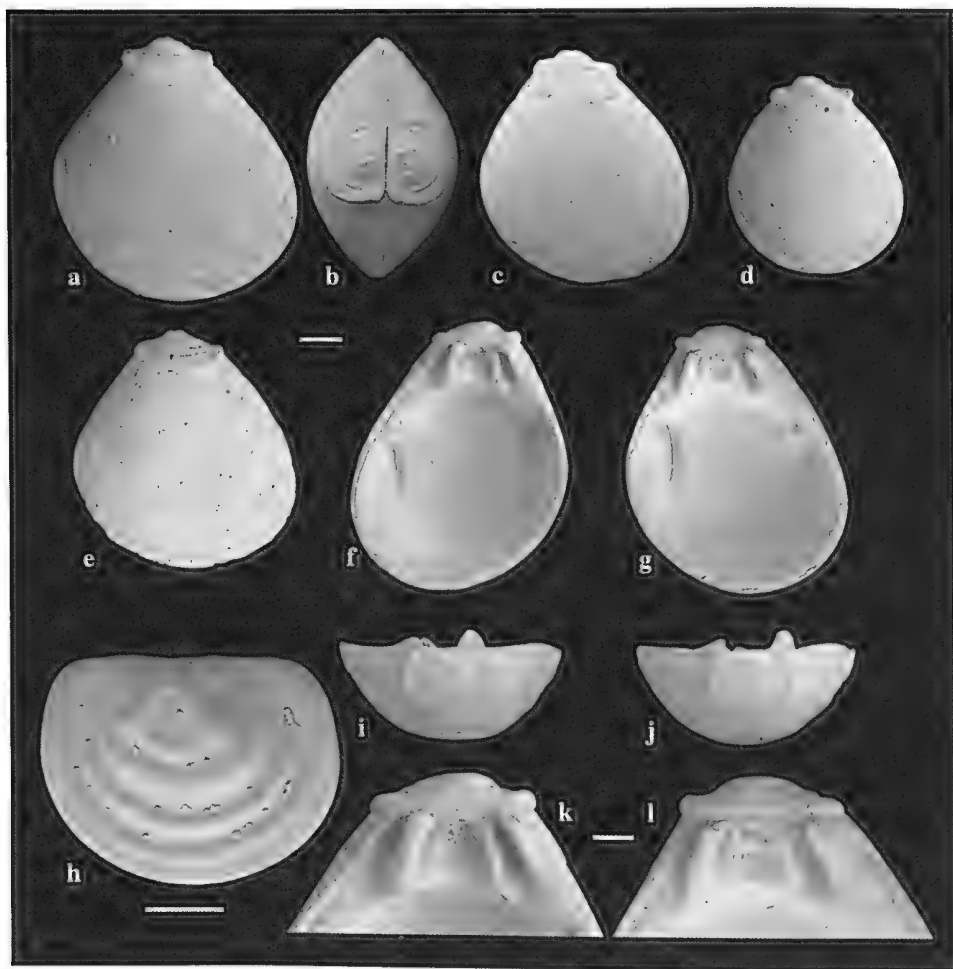


Fig. 15. *Austrocardiella trifoliata*. a, b, *Condyllocardia trifoliata* lectotype C019393, Masthead Is., Queensland. c, *Condyllocuna cambrica* lectotype C025120, Chinamans Beach, Sydney, New South Wales. d, *Benthocardiella vitrea* lectotype C090566, Narrabeen Beach, Sydney, New South Wales. e–l, C366859, off Sow and Pigs Reef, Sydney, New South Wales. Scale bars: a–g, i, j, 200 μ m; h, k, l, 100 μ m.

Table 8. Measurements of specimens of *Austrocardiella trifoliata* (Hedley, 1906b)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condylocardia trifoliata</i> , lectotype, C019393 (Fig. 15a, b)	1.12	1.22	0.41	0.37	1.51
<i>Benthocardiella vitrea</i> , lectotype, C090566 (Fig. 15d)	0.80	0.90	0.38	0.36	1.11
<i>Condylocardia cambrica</i> , lectotype, C025120 (Fig. 15c)	0.90	1.07	0.39	0.39	1.15
<i>Austrocardiella trifoliata</i> , C381942	1.15	1.29	0.43	0.38	1.51
	1.13	1.26	0.44	0.38	1.49
	1.10	1.20	0.43	0.44	1.25
	0.96	0.97	0.42	0.31	1.55
	1.10	1.28	0.43	0.42	1.31
<i>Austrocardiella trifoliata</i> , C366868	1.04	1.17	0.48	0.39	1.33
	1.02	1.29	0.44	0.42	1.21
	1.46	1.28	0.43	0.46	1.59
	0.86	0.85	0.45	0.30	1.43
	0.86	0.94	0.43	0.29	1.48

Laserson (1953) described *Benthocardiella vitrea* as new with the note ‘...very close to *C. isosceles* Cotton, a South Australian species, but *C. isosceles* is practically equilateral and has a multifoliate prodissoconch rising to a peak’. *Austrocardiella isosceles* has been shown herein to have a single indentation in the prodissoconch, not three as mentioned by

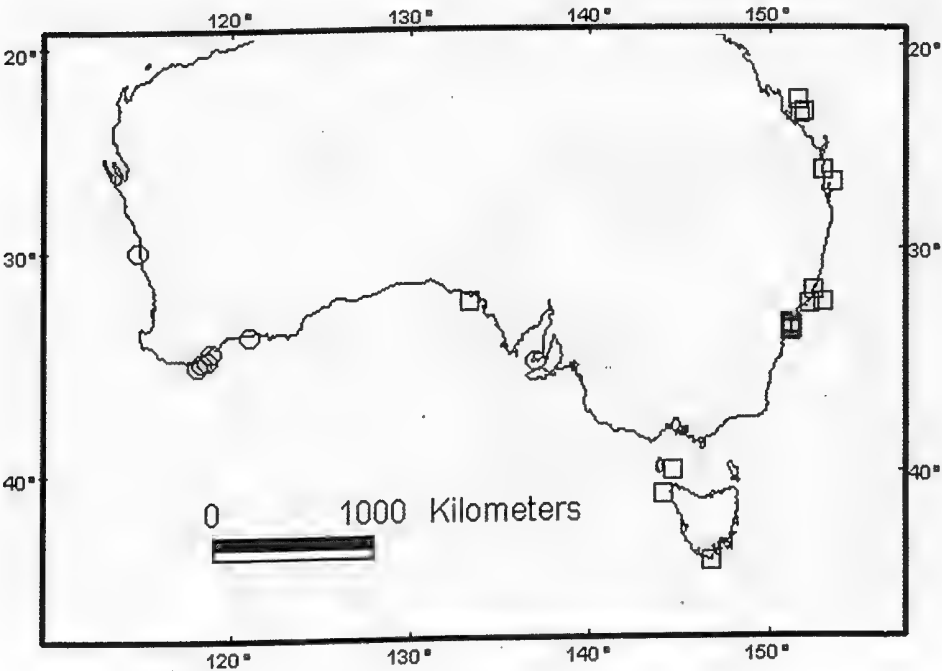


Fig. 16. Distribution of *Austrocardiella trifoliata* (□) and *A. isosceles* (O).

Laseron. Further, the shape of *A. trifoliata* is not inequilateral, but quite similar to *A. isosceles*. Two of the three specimens in the primary type lot for *B. vitrea* have a trifoliate prodissoconch, the third specimen is *Mysella ovata* (see below). The illustration for *B. vitrea* in Laseron's paper is unmistakably *A. trifoliata*, and the description of two to three cardinals in the right valve is not consistent with *Mysella ovata*. For some reason Laseron did not observe the trifoliate pattern on the prodissoconch in these specimens, but did observe the commarginal ribs of the prodissoconch, a character never observed in the genus *Benthocardiella*.

The distribution gaps in southern New South Wales, Victoria and parts of South Australia may be a result of inadequate sampling of these tiny bivalves, or the South Australian record might be in error.

Genus *Benthocardiella* Powell, 1930

Benthocardiella Powell, 1930: 533. Type species (original designation): *Benthocardiella pusilla* Powell, 1930.

Diagnosis

Shell less than 1.5 mm, round to oval; prodissoconch smooth, with single, central elevation, rim with a heavy bulge. Hinge with cardinal CA3 curved, free standing and dorsally arched into CA3a,b; CA2 free. Hinge plate very narrow. Externally sculptured with commarginal growth lines, ventral margin smooth to dentate.

Remarks

Species of *Benthocardiella* are generally smooth, with a large, smooth, slightly elevated prodissoconch. The ventral margin may be dentate or smooth. The hinge consists of slightly detached cardinals CA3a,b well separated from the shell margin, except at the point where they join. Posteriorly, a small PC3 lies adjacent to the ligament. In the left valve, the anterior cardinal CA2 is detached. Dorsally (anteriorly and posteriorly to CA2) there is a dorsally divided small tooth that is possibly a CA4a,b. The posterior cardinal is obsolete in the left valve. There is both an anterior and a posterior lateral tooth in each valve. These characters are all concordant with the characters of *B. pusilla*, type species of *Benthocardiella*.

There is a superficial resemblance in hinge characters between the species here included in *Benthocardiella* and species of *Cyamiomactra* Bernard, 1897b and *Cyamium* Philippi, 1845 (Cyamiidae). In an early paper Hedley (1906a) placed *Cyamiomactra* (and *Cyamium*) in Crassatellidae. Thiele (1934) placed the Cyamiidae in a new superfamily Cyamiacea together with Neoleptonidae Thiele, 1934 and Sportellidae Dall, 1899, a classification followed by Chavan (1969). It is difficult to determine the difference between the hinge configuration of Cyamiidae and Neoleptonidae, except that they are transposed in relation to each other. Apparently the transposition of hinges can happen even within species (Moore, 1969, p. N57) and seems to be especially frequent in the Astartidae and Crassatellidae, both close relatives of the Condyllocardiidae.

The two species described below are somewhat tentatively included in the Condyllocardiinae, because the hinge teeth configuration matches that of other species in the family, especially *Condylocardia* and *Condyllocuna* species. The prodissoconch is also very similar to other condyllocardiines.

Benthocardiella burtonae n. sp.

(Figs 17a–g, 19)

Material examined

Holotype. (Fig. 17a). (1v) C388190, Collaroy Beach, N of Sydney, New South Wales, 33°43.7'S 151°18'E, shell sand, 1950, coll. J. Voorwinde.

Paratypes. (Fig. 17b–g). (7v) C379873, Collaroy Beach, N of Sydney, New South Wales, 33°43.7'S 151°18'E, shell sand, 1950, coll. J. Voorwinde.

Other material examined. **New South Wales.** Off Port Stephens, off lighthouse, 32°42.5'S 152°15'E, 45–73 m, 1950, C379875 (7v). **Sydney area:** Manly, 33°48.2'S 151°17'E, 1926, C379876 (4v); Chinamans Beach, 33°48.97'S 151°14.87'E, 1950, C379874 (1v); off Balmoral 33°49.5'S 151°15.4'E, 3.5–9 m, 1950, C379870 (1v); Balmoral Beach, 33°49.7'S 151°15.03'E, 1957, C379869 (2v). Green Cape, S side of tip, 37°16'S 150°3'E, 2–4 m, mixed algae, exposed side, 13 Feb. 1973, C379871 (1v).

Description

Shell. Maximum length 1.42 mm, maximum height 1.42 mm, equilateral, orthogyrate, circular, translucent or opaque white. Inflation ratio, 1.27–1.70.

Prodissoconch. Maximum length 500 µm, consisting of prodissoconch I (discontinuity line between prodissoconch I and II not observed). Prodissoconch I smooth but slightly raised towards umbo, rim thickened.

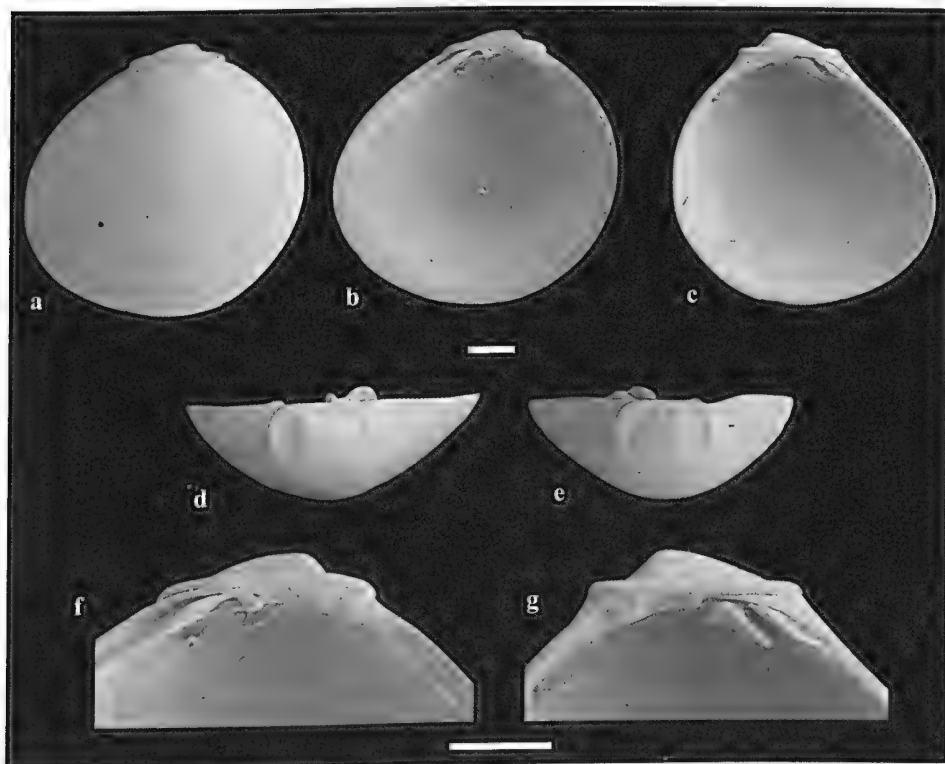


Fig. 17. *Benthocardiella burtonae* n. sp. a, Holotype C388190. b, d, f and c, e, g, same valves, paratypes C379873. All Collaroy Beach, Sydney, New South Wales. Scale bars: a–e (upper scale) and f, g (lower scale); 200 µm.

Table 9. Measurements of specimens of *Benthocardiella burtonae* n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Benthocardiella burtonae</i> holotype C388190 (Fig. 17a)	1.17	1.12	0.40	0.42	1.39
<i>Benthocardiella burtonae</i> , paratypes, C379873 (Fig. 17b)	1.20	1.13	0.44	0.37	1.62
(Fig. 17c)	1.09	1.12	0.43	0.41	1.33
	1.26	1.22	0.41	0.37	1.70
	1.38	1.42	0.50	0.49	1.41
	1.42	1.39	0.43	0.56	1.27

Dissoconch. Lunule and escutcheon absent. Sculpture consists of weak commarginal growth lines; inner margin smooth. Hinge plate narrow. Two smooth lateral teeth in each valve. Right valve anterior lateral (LAI) and posterior lateral (LPIII) long. Left valve anterior lateral (LAI) long and posterior lateral (LPII) short. Right valve anterior cardinal (CA3) arched, divided into anterior cardinal elements CA3a,b. Posterior cardinal (CP3) vestigial. Left valve anterior cardinals (CA2 and CA4) present, CA4 divided into anterior cardinal elements CA4a,b. Posterior cardinal (CP4) vestigial. Internal ligament 50 µm long, triangular, in resilium.

Dimensions. See Table 9.

Distribution

The few records of this species occur between Port Stephens and Green Cape, New South Wales, from shallow subtidal to 73 m. Habitat unknown. This species is only known from shells.

Remarks

Benthocardiella burtonae differs from *B. darwinensis* in being more inflated (see inflation ratio in Table 9), with a longer and less arched and detached CA3. The prodissoconch of *B. burtonae* is significantly larger than *B. darwinensis* (0.44 ± 0.04 mm for *B. burtonae* versus 0.36 ± 0.05 mm for *B. darwinensis* ($X \pm SD$, $n=5$; t -test, $p < 0.01$)). The inner ventral margin is smooth in *B. burtonae* and denticulate in *B. darwinensis*.

Etymology

Named for Ms Pat Burton in appreciation of her years of sorting micro-bivalves as a volunteer in the Malacological section of the Australian Museum, Sydney.

Benthocardiella darwinensis n. sp.

(Figs 18a–h, 19)

Material examined

Holotype. C388191 (Fig. 18a) off Emery Point, Darwin, Northern Territory, 12°27'S 130°49'E, on sandbar, 25 Oct. 1969, coll. P. H. Colman.

Paratypes. C379877 (8v), off Emery Point, Darwin, Northern Territory, 12°27'S 130°49'E, on sandbar, 25 Oct. 1969, coll. P. H. Colman. C379878 (Fig. 18c, e, g) (4v); NTM P14470 (Fig. 18b, d, f, h) (1v), Sandbar No.1, Darwin, Northern Territory, 12°26'S 130°48'E, 14 Nov. 1970, coll. O. J. Cameron.

Description

Shell. Maximum length 1.21 mm, maximum height 1.04 mm, equilateral, orthogyrate, ovate, translucent and uniformly coloured, white to pink. Inflation ratio, 1.56–2.17.

Prodissoconch. Maximum length 370 μm , consisting of prodissoconch I (discontinuity segregating prodissoconch I and II not observed). Prodissoconch I smooth but slightly raised towards umbo, rim thickened.

Dissoconch. Lunule and escutcheon absent. External sculpture of commarginal growth lines only. Inner margin denticulate with 27 denticles ($n=2$). Hinge plate narrow. Two smooth laterals in each valve. Right valve anterior lateral (LAI) and posterior (LP III) long. Left valve anterior lateral (LAI I) long and posterior lateral (LP II) short. Right valve anterior cardinal (CA3) arched, subdivided into cardinal elements CA3a,b. Posterior cardinal (CP3) vestigial. Left valve with two anterior cardinals (CA2 and CA4), CA4 dorsally divided into anterior element CA4a and posterior element CA4b. Posterior cardinal (CP4) vestigial. Internal ligament 50 μm long, rounded, in resilium.

Dimensions. See Table 10.

Distribution

Off Darwin, Northern Territory. Found in sediment from sandbars. This species is only known from shells.

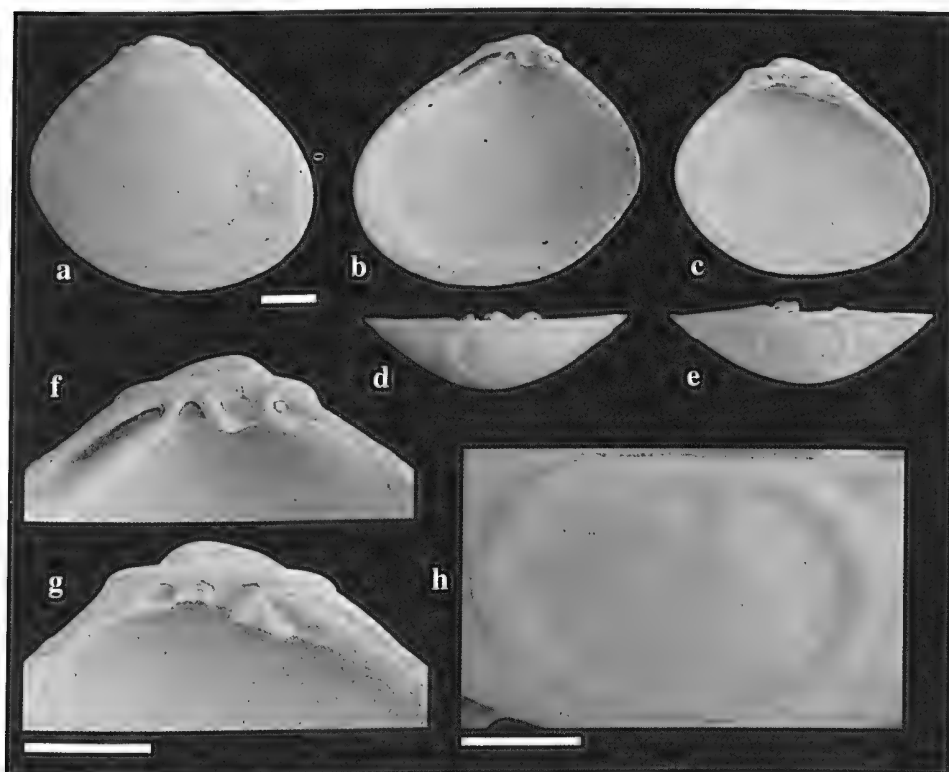


Fig. 18. *Benthocardiella darwinensis* n. sp. a, Holotype C388191, off Emery Point, Darwin, Northern Territory. b, d, f, h, Paratype NTM P14470, c, e, g, paratype; C379878, Sandbar No. 1, Darwin, Northern Territory. b, d, f, h' and c, e, g, Same valves. Scale bars: a–e and f, g, 200 μm ; h, 100 μm .

Table 10. Measurements of specimens of *Benthocardiella darwinensis* n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Benthocardiella darwinensis</i> , holotype C388191 (Fig. 18a)	1.03	0.91	0.32	0.33	1.56
<i>Benthocardiella darwinensis</i> , paratypes, C379878 (Fig. 18b, d, f, h)	1.04	0.89	0.30	0.24	2.17
	1.19	0.99	0.37	0.34	1.75
	1.21	1.04	0.37	0.30	2.02
	1.07	0.87	0.34	0.27	1.98

Remarks

Benthocardiella darwinensis is more elongate than *B. burtonae*, slightly more solid and with a dentate ventral margin. The cardinal CA3 is very similar to *B. burtonae* but more arched and attached to the dorsal part of the hinge plate. *Benthocardiella darwinensis* is pinkish coloured when fresh.

Etymology

Named after the type locality, Darwin.

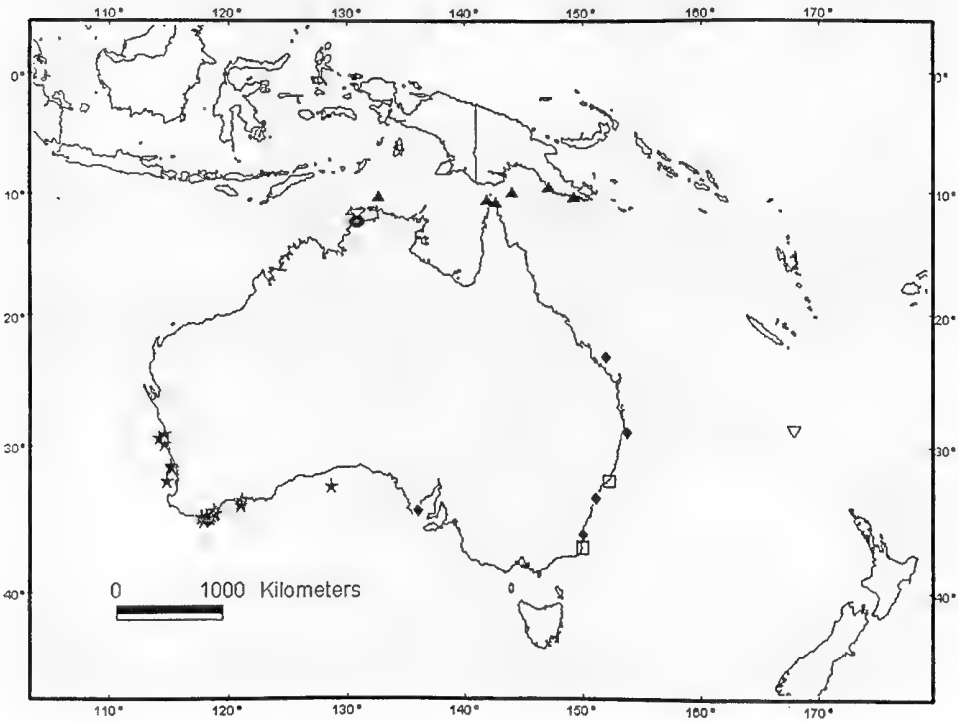


Fig. 19. Distribution of *Benthocardiella burtonae* n. sp. (□), *B. darwinensis* n. sp. (●), *Isodontocardia microcardia* n. sp. (▲), *Condyllocuna tricoso* n. sp. (◆) and *Austrocardiella pouli* n. sp. (★).

Genus *Condyllocuna* Iredale, 1936

Condyllocuna Iredale, 1936: 272. Type species (original designation): *Condyllocardia projecta* Hedley, 1902.

Diagnosis

Shell small (less than 1.5 mm). Prodissoconch with three radiating indentations, anterior and posterior end non-auricular, rim bulging. External dissoconch structure commarginal ribs. Ventral margin denticulate. Hinge teeth more or less developed. Left valve anterior cardinal CA2 absent.

Remarks

Iredale (1936) erected this genus based on the difference in hinge teeth and commarginal ribbing from *Condyllocardia*. He included *Condyllocardia ovata* Hedley, 1906a (here included in *Mysella* Angas, 1877), *Condyllocardia trifoliata* Hedley, 1906b (here included in *Austrocardiella*) and *Condyllocuna projecta*, which he selected as type.

Although *Condyllocuna minuta* Laseron, 1953: 41, figs 14, 14a has commarginal ribs, the hinge teeth configuration is very different from other species in *Condyllocuna* and is better placed as a species of *Warrana* Laseron, 1953. The taxon is here excluded from the condyllocardiines and will be dealt in a subsequent revision of the Australian Cuninae (Middelfart, unpublished data.).

Three species of *Condyllocuna* occur in New Zealand (Spencer and Willan 1996).

Condyllocuna projecta (Hedley, 1902)

(Figs 20a–l, 21)

Condyllocardia projecta Hedley, 1902: 316, text fig. 57 (type locality: off Watsons Bay, Port Jackson, Sydney, New South Wales. 33°50.7'S, 151°16.7'E, pre 1902, coll. Australian Museum party. Holotype C013247 (Fig. 20a) 1 valve). – Pritchard & Gatliff, 1904: 231; May, 1909: 54; Hedley, 1918: M17, no. 165; May, 1921: 17; May, 1923: no. 12, pl. 7, fig. 12; Macpherson & Chapple, 1951: 17.

Condyllocuna projecta (Hedley, 1902). Iredale, 1936: 272. – Laseron, 1953: 40, fig. 16; Kershaw, 1955: 296; Macpherson & Gabriel, 1962: 321; Jansen, 1995: 101, fig. 426; Lamprell & Healy, 1998: 170, fig. 481.

Other material examined. **Queensland.** Great Barrier Reef: Heron Is. 23°26'S 151°57'E: W side, 1950, C380307 (7v); 6 m, 1967, C380328 (3v); 8 m, 1967, C380298 (14v); off S side, 1–8 m, in coral rubble with algal layer off reef, 26 Dec. 1976, C380305 (2v); S side, rubble just below beach rock, low tide, 2 Jan. 1977, C380306 (9v); NW corner of reef, intestines of *Holothuria atra*, Aug. 1985, C380289 (11v). Wistari Reef, N side, 23°28'S 151°53'E, 4.5 m, in rubble and very short algae, over exposed edge, 28 Dec. 1976, C380294 (2v). **New South Wales.** 12 km E of Cakora Point, S of Yamba, 29°39.8'S 153°26.4'E, 55 m, 22 Feb. 1972, C380146 (3v). 15 km NE of Coffs Harbour, 30°15'S 153°19'E, 73–82 m, 1967, C380148 (1v). 14 km E of Coffs Harbour, 30°18.4'S 153°17.7'E, 76 m, 22 Feb. 1972, C380147 (1v). Off Crowdy Head, 32°38.9'S, 153°0.8'E, 91 m, 16 Dec. 1957, C380302 (2v). North Fingal Bay, near Port Stephens, 32°44.75'S 152°10.5'E, 1950, C380150 (5v). 9–12 km NE of Cape Three Points, 33°32.5'S 151°31.4'E, 75–91 m, sticky mud and shell, 25 Feb. 1898, C16909 (2v). *Sydney area:* Narrabeen Beach, 33°42'S 151°18'E, 1951, C315605 (2pr); Collaroy Beach, 33°43.7'S 151°18'E, 1950, C366901 (2v) and C366905 (12v); Manly Beach, 33°47.7'S 151°17.19'E, 15 May, 1916, C366902 (1pr), beach shell sand, 1950, C380311 (12v), and 1957, C380143 (1v); Fairlight, 33°48.2'S 151°16.4'E, 4–7 m, 1955, C366912 (1v); off Fairlight Beach, 33°48.2'S 151°16.4'E, 6–9 m, in shell rubble, 28 Feb. 1981, C380303; 33°48.5'S 151°16.5'E, 1950, C366911 (3pr); Little Manly Beach, 33°48.5'S 151°17.2'E, 1950, C366904 (9v); North Harbour, 33°48.5'S 151°16.5'E, 4 m, weed, 1950, C380312 (2v); off Chinamans Beach, 33°48.97'S 151°14.87'E, 3.5–7.5 m, 1967, C366908 (19v), 4–8 m, 1967, C380145 (8v); Watsons Bay, off Green Point, 33°50.5'S 151°16.5'E, 14.5 m, 1873, C380142 (1pr); off Watsons Bay, 33°50.7'S 151°16.7'E, 1902, C13247 (4v); off Bottle and Glass Rocks, 33°50.94'S 151°16.13'E,

14 m, from sand in bottle, 22 May 1886, C366909 (2pr); South Coogee, 33°55.5'S 151°15.6'E, 10 m, algae, 12 Aug. 1979, C380317; 2 km SE of Long Bay, 33°58.43'S 151°16.32'E, 29 m, 27 Sep. 1972, C380308 (1pr); Bate Bay, Cronulla Beach, 34°2.5'S 151°10'E, 1967, C366907 (3v); Boat Harbour, N of Cronulla, 34°2.5'S 151°12'E, 2 m, rock and shell rubble in gully between rock platforms, 3 Nov. 1982, C366913 (1v); Gunnamatta Bay, Port Hacking, 34°3.95'S 151°8.55'E, 1951, C90588 (48v); Port Hacking, SW end of Gunnamatta Bay, 34°4.3'S 151°8.7'E, in channel, 1950, C366893 (3v). 26 km E off Wollongong, 34°25'S 151°15'E, 183 m, Aug. 1902, C18230. (5v). 8–13 km off Port Kembla, 34°27.9'S 151°4.5'E, 115–137 m, mud and pebbles, 18 March 1898, C13249 (4v). Warri Beach, Gerringong, 34°44.3'S 150°50'E, 1950, C380319 (3v). Pebbly Beach, 35°36.8'S 150°19.7'E, 1980, C366900 (1v). Bermagui, Shelly Beach, 36°25'S 150°5'E, 1967, C380151 (12v). Off Green Cape, 37°15.5'S 150°12'E, 110 m, muddy sand bottom, 1950, C366903 (1v). **Victoria.** Bass Strait, 36 km S of Cape Conran, 38°8.5'S 148°43.5'E, 107 m, May 1969, C380300 (1v). Bass Strait, 44 km S of Marlo, 38°12'S 148°35'E, 146 m, flat outer shelf, 7 May, 1969, C380310 (8v). Sandy Point, Western Port, just N of North Arm, 38°24.3'S 145°14.2'E, 7.5 m, sandy mud and shell, 28 Feb. 1977, C380321 (2prs). **Tasmania.** Bass Strait, Marawah (Green Point), 41°10.82'S 144°52.79'E, 27 Dec. 1996, C380291 (1v). Off Bicheno, 41°50'S 148°17.3'E, 33 m, fine medium sand, 24 March 1973, C380301 (3v). Pirates Bay, Eaglehawk Neck, 43°1'S 147°56'E, under intertidal rocks, low tide, 30 March 1970, C366898 (1pr). W of Port Davey, 43°20.3'S 145°48.2'E, 82 m, 9 April 1973, C380314 (1v). S of D'Entrecasteaux Channel, 43°40.4'S 146°50.4'E, 104 m, 2 April 1973, C380290 (3v). **Western Australia.** Off Albany: 35°6.4'S 118°10.6'E, 72 m, fine sand, 12 March 1980, C380283 (1v); 35°22.6'S 118°10.2'E, 120 m, 12 March 1980, C380285 (1v); 35°4.1'S 118°6.4'E, 62 m, fine sand, 16 March 1980, C380286 (1v). Off North West Cape, 21°57.3'S 113°52'E, 88 m, fine sand and mud, Sep. 1981, C380293 (1v); off North West Cape, 22°58'S 113°41.2'E, 78 m, fine sand, Sep. 1981, C380292 (5v). **Coral Sea.** Middleton Reef, 29°27.6'S 159°6.7'E, 8 m, sand with algae in lagoon, 6 Dec. 1987, C380296 (1v). Elizabeth Reef, 29°55.4'S 159°2.7'E, rubble bank and sand flats, low water spring tide, 10 Dec. 1987, C380287 (22v). Elizabeth Reef, 29°56.2'S 159°2.4'E, 10 m, in dead coral on lagoon bommies, 12 Dec. 1987, C380295 (1v). Off NE side, 31°31'S 159°5'E, 27.5 m, 1912, C380327 (1v). Signal Point, 31°31.5'S 159°3.9'E, on short red algae on rocks, mean tide level, 21 April 1978, C380326 (2v). 31°32.5'S 159°4.7'E, 1912, C380299 (31v). S end of lagoon, 31°34'S 159°4.4'E, algae on outer reef crest, low tide, 23 April 1978, C380297 (1v).

Description

Shell. Maximum length 1.28 mm, maximum height 1.13 mm, inequilateral, with umbo equidistant from centre and end of shell, orthogyrate, translucent or opaque white. Inflation ratio, 1.54–2.00.

Prodissoconch. Maximum length 320 µm consisting of prodissoconch I and II. Prodissoconch I with three radiating indentations and prodissoconch II with commarginal pattern and thickened rim.

Dissoconch. Lunule and escutcheon short and broad, mostly smooth. Outline triangular, anterior end extended and dorsal anterior and posterior slope concave or straight, making the prodissoconch appear positioned on neck in a few specimens. Anterior end broadly rounded and posterior end sharply bent or slightly truncate. External sculpture of up to 21 commarginal ribs. Inner margin denticulate with 18 denticles. Hinge plate short but strong. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half dorsal slopes. Right valve anterior cardinal tooth (CA3) strong. Posterior cardinal tooth (CP3) strongly curved, subdivided into cardinal elements CP3a,b. Left valve anterior cardinal tooth (CA4) present, subdivided into cardinal elements CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP2 much larger than CP4. Internal ligament 77 µm long, rounded, in resilium.

Dimensions. See Table 11.

Distribution

Queensland, New South Wales, Lord Howe Island, Victoria, Tasmania and Western Australia, low intertidal to 183 m depth. Found in algae washings, dead coral, rock, rubble, shell, sand, fine sand, muddy sand and mud. This species is only known from shells.

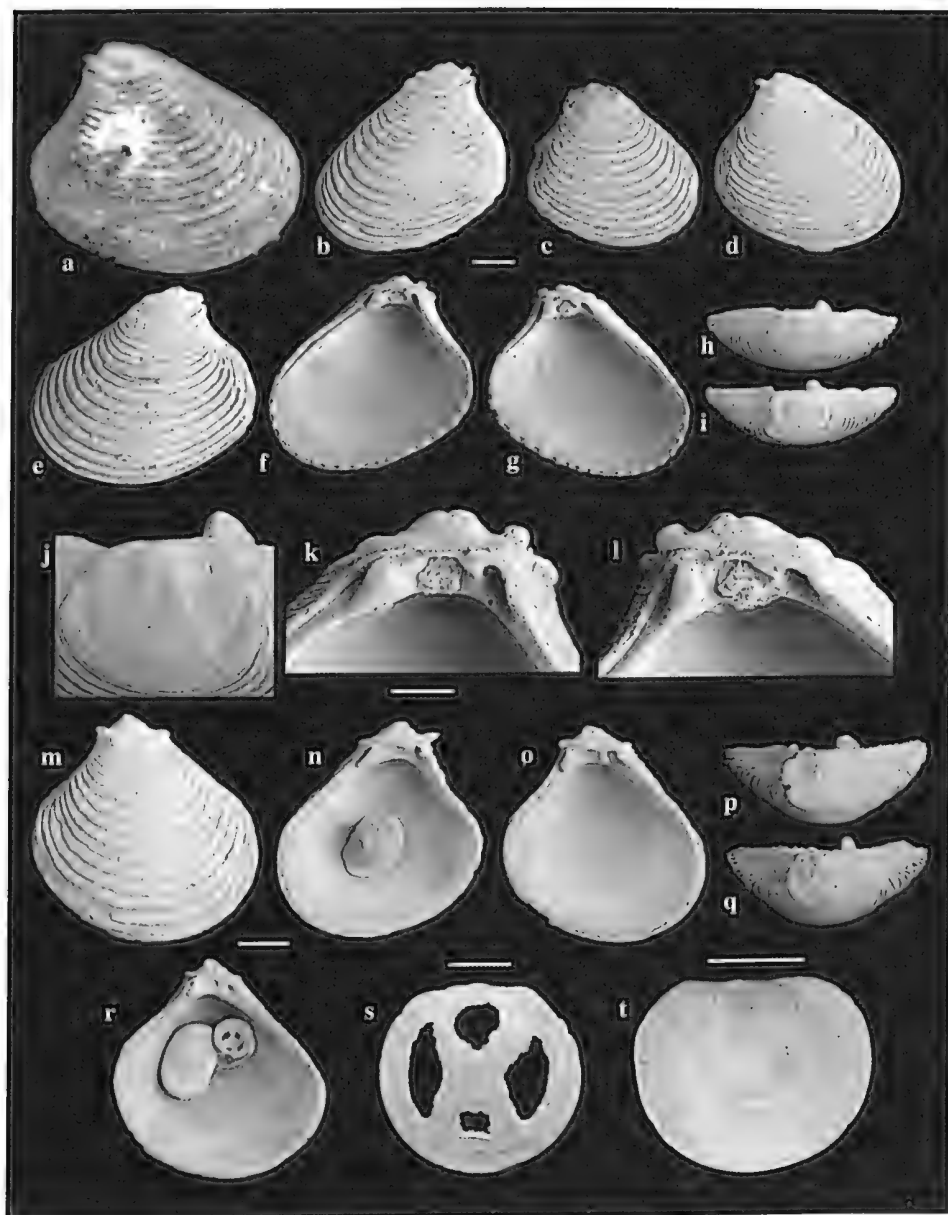


Fig. 20. *Condyllocuna projecta* and *Condyllocuna jimbecki* n. sp. *a*, *Condyllocuna projecta* holotype C013247 off Watsons Bay, Sydney, New South Wales. *b*, C315605, Narrabeen, New South Wales. *c*, C380317, Coogee, New South Wales. *d*, *h-j*, C380151, Bermagui, New South Wales. *e-g*, *k*, *l*, C366908, Sydney Harbour, New South Wales. *m-t*, *Condyllocuna jimbecki* n. sp. *m*, Holotype NMNZ M.273102, N of Norfolk Island. *n-t*, Paratypes C388215, N of Norfolk Island. Scale bars: *a-i* and *m-r*, 200 μ m; *j-l* and *t*, 100 μ m; *s*, 50 μ m.

Remarks

Condyllocuna concentrica (Bernard, 1896) from Stewart Island, New Zealand is closely similar to *C. projecta*. However, the prodissoconch is different and the commarginal ribs are closer and more numerous in *C. concentrica*. *Condyllocuna annieae* may be readily

Table 11. Measurements of specimens of *Condyllocuna projecta* (Hedley, 1902)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condyllocuna projecta</i> , holotype, C013247 (Fig. 20a)	1.28	1.13	0.29	0.32	2.00
<i>Condyllocuna projecta</i> , C380145	1.04	0.99	0.32	0.27	1.93
	1.15	1.09	0.28	0.33	1.74
	1.09	1.01	0.32	0.35	1.56
	1.09	1.05	0.32	0.35	1.56
	1.11	1.10	0.28	0.36	1.54

distinguished from *C. projecta* by its much larger prodissoconch (see Remarks under *C. annieae*). *Condyllocuna jimbecki* is also very similar to *C. projecta* (see Remarks under *C. jimbecki*).

The absence of records from South Australia and parts of Western Australia might be due to lack of sampling or may indicate the presence of cryptic taxa.

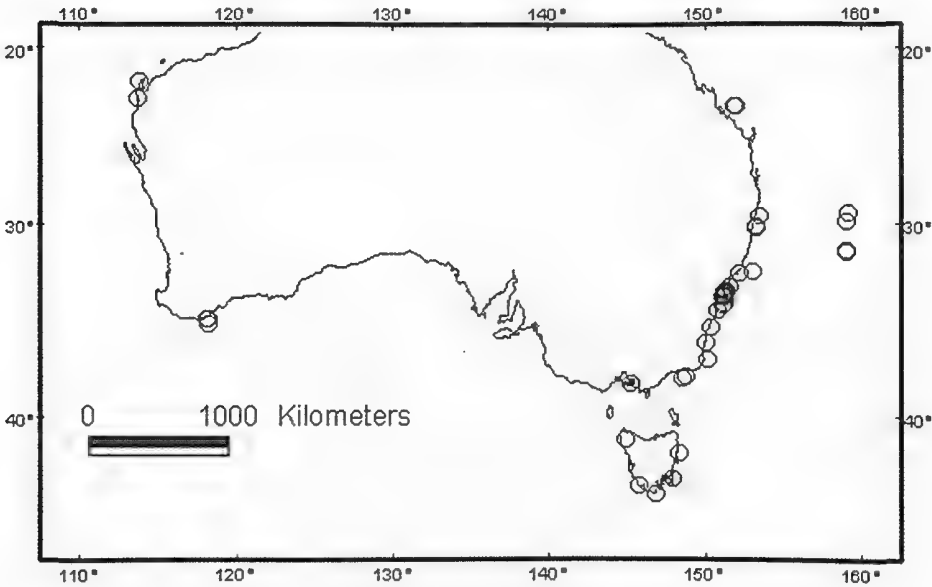


Fig. 21. Distribution of *Condyllocuna projecta*.

Condyllocuna annieae n. sp.
(Figs 12, 22a–f)

Material examined

Holotype. C388200 (Fig. 22a) (1v), Norfolk Island, 29°2'S 167°57'E, 1910, coll. R. Bell, ex. T. Iredale coll.
Paratypes. C380329 (Figs 22b–f) (31pr, 11v), NMNZ M.273096 (4v), Norfolk Island, 29°2'S 167°57'E, 1910, coll. R. Bell, ex. T. Iredale coll.

Other material examined. **Norfolk Island.** Off Duncombe Bay, 29°S 167°56'E, 31 m, 1940, C380330 (7v). 28°56'S 167°58'E, N of Norfolk Island, 38 m, 9 July, 1962, NMNZ M.224876 (20+ pr, v). 28°54'S 167°59'E, N of Norfolk Island, 33 m, 9 July 1962, NMNZ M.224580 and NMNZ M.225150 (20+ pr, v). 29°20'S 168°09'E, E of Norfolk Island, 201 m, 11 July 1962, NMNZ M.224790. 29°19'S 168°07'E, off Norfolk Island, 110 m, 11 July 1962, NMNZ M.225021 (9prs; 11v).

Description

Shell. Maximum length 1.15 mm, maximum height 1.21 mm, slightly inequilateral, orthogyrate, translucent or opaque white. Inflation ratio, 1.23–1.59.

Prodissoconch. Maximum length 520 μ m, consisting of prodissoconch I and II. Prodissoconch I with three radial indentations, prodissoconch II with few commarginal rings and thickened rim.

Dissoconch. Lunule and escutcheon broad and very distinctly smooth. Outline slightly triangular, with slightly elongate, broadly rounded anterior and short, slightly angled posterior end. Dorsal slopes appear straight in exterior aspect. Exterior sculpture of up to 24 commarginal ribs. Inner margin denticulate with 16 denticles. Hinge plate present. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half dorsal slopes. Right valve anterior cardinal tooth (CA3) prominent and detached from anterior lateral tooth. Posterior cardinal tooth (CP3) dorsally recurved, divided into cardinal elements CP3a,b. Left valve anterior cardinal tooth (CA4) dorsally recurved, divided into CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP2 much larger than CP4. Internal ligament 62 μ m long, rounded, in resilium.

Dimensions. See Table 12.

Distribution

Norfolk Island, 31–201 m. Habitat unknown. This species is only known from shells.

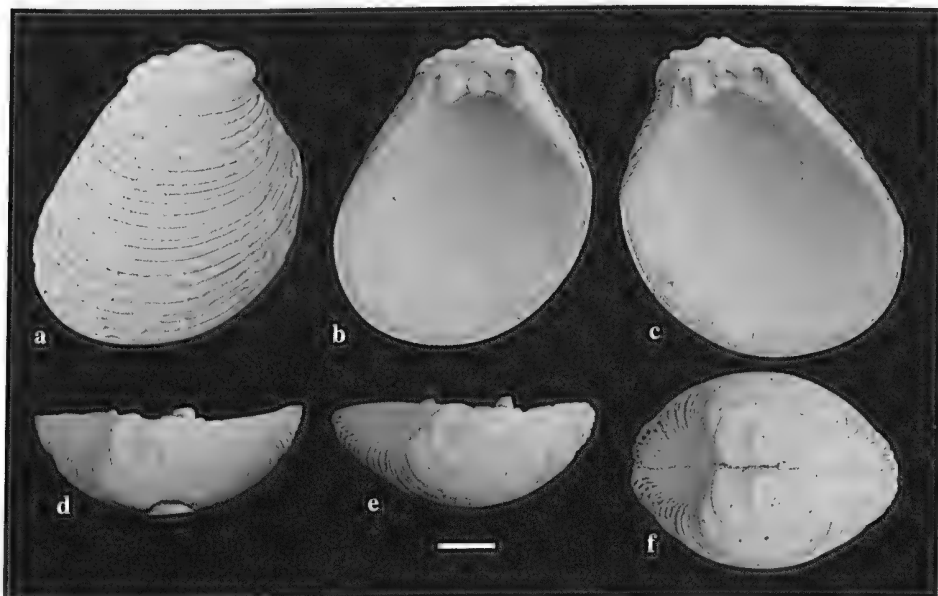


Fig. 22. *Condyllocuna annieae*. a, Holotype C388200, Norfolk Island. b–f, Paratypes C380329, Norfolk Island. Scale bar: 200 μ m.

Table 12. Measurements of specimens of *Condyllocuna annieae* n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condyllocuna annieae</i> holotype, C388200 (Fig. 22a)	0.96	1.05	0.46	0.39	1.23
<i>Condyllocuna annieae</i> , paratypes, C380329	1.15	1.16	0.51	0.43	1.34
	1.15	1.21	0.52	0.41	1.40
	1.05	1.08	0.47	0.37	1.42
	1.05	1.09	0.50	0.33	1.59
	1.05	1.13	0.49	0.36	1.46

Remarks

Condyllocuna annieae can be readily distinguished from *C. projecta* by the significantly larger size of the prodissoconch (0.49 ± 0.02 mm in *C. annieae* and 0.30 ± 0.02 mm in *C. projecta*; $X \pm SD$, $n=6$; t -test, $p < 0.01$). The species is slightly less inequilateral than *C. projecta*. The prodissoconch of *Condyllocuna jimbecki* n. sp. is smaller.

Etymology

Named after the author's partner, Ms Annie Bowen, in recognition of her patience and help over the years.

Condyllocuna jimbecki n. sp.

(Figs 12, 20m–t)

Material examined

Holotype. NMNZ M.273102 (Fig. 20m) 28°59'S 167°58'E, N of Norfolk Island, 38 m, Sep. 1962.

Paratypes. NMNZ M.273103 (22pr, 11v), C388215 (6prs, 5v and valves in Fig. 20n–t), 28°59'S 167°58'E, N of Norfolk Island, 38 m, Sep. 1962.

Other material examined. **Norfolk Island**. Off Duncombe Bay, 29°S 167°56'E, 31 m, 1940, C380324 (1v). 29°2'S 167°57'E, 1910, C380322 (8v). Emily Bay, Kingston, 29°4'S 167°58'E, short mixed algae from rock platform, 16 Sep. 1975, C380325 (2v). 28°56'S 167°58'E, 38 m, 9 June 1962, M.273101 (1pr, 1v). 28°54'S 167°59'E, 33 m, 9 June 1962, NMNZ M.273104 (4pr, 1v). 29°19'S 168°07'E, 110 m, 11 June 1962, NMNZ M.273105 (9pr, 8v). 29°20'S, 168°09'E, 201 m, 11 June 1962, NMNZ M.273106 (7pr).

Description

Shell. Maximum length 0.98 mm, maximum height 1.0 mm, equilateral, orthogyrate and white. Inflation ratio, 1.33–1.62.

Prodissoconch. Maximum length 320 μ m, consisting of prodissoconch I and II. Prodissoconch I, with three radiating indentations, prodissoconch II smooth with sharp rim.

Dissoconch. Lunule and escutcheon large and conspicuously smooth. Outline triangular, with anterior end very slightly extended and broadly rounded, posterior end is slightly recurved and angled. External sculpture consists of up to 18 strong commarginal ribs. Inner margin smooth. Hinge plate short and narrow. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAIII, LAII) and posterior lateral teeth (LPIII, LPII) longer than half length of dorsal slopes. Right valve anterior cardinal tooth (CA3) prominent but narrow and oblique. Both posterior cardinal tooth (CP3) and left valve anterior cardinal tooth (CA4) dorsally recurved, divided into cardinal elements (CP3a,b;

Table 13. Measurements of specimens of *Condyllocuna jimbecki* n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condyllocuna jimbecki</i> , holotype, NMNZ M.273102 (Fig. 20m)	0.92	0.88	0.29	-	-
<i>Condyllocuna jimbecki</i> , paratypes, C388215	0.84	0.82	0.32	0.26	1.62
	0.90	0.92	0.32	0.32	1.41
	0.96	1.00	0.28	0.36	1.33
	0.98	1.00	0.32	0.36	1.36
	0.96	1.00	0.32	0.34	1.41

CA4a,b). Posterior cardinal teeth (CP2 and CP4) present, CP2 most prominent. Internal ligament 70 µm long, in resilium.

Dimensions. See Table 13.

Reproduction

Two to six brooded embryos observed in dried specimens (e.g. C388215).

Distribution

Norfolk Island, found on the shelf from the intertidal zone (probably washed ashore) to 201 m depth. Habitat unknown. This species is only known from shells.

Remarks

Some embryos were discovered in dried specimens, which testifies to the development of the prodissoconchs of condyllocardiines (Fig. 20r). These females contained embryos in the prodissoconch I (Fig. 20s) and II (Fig. 20t) stage. Since the animals were dried, all organic material had decomposed leaving only the calcified structures. The remaining structure in embryos with prodissoconch I consists of a circular shell with four 'holes' separated by an X-shaped bridge. These 'holes' are calcified in more developed embryos (Fig. 20t) and create the pattern seen in species of, for example, *Condyllocuna*.

Prodissoconch I in *C. jimbecki* has a smaller ventral 'hole' to that of *C. projecta*. Prodissoconch I is also shorter (approximately 120 µm in *C. jimbecki* and 150 µm in *C. projecta*). Further, the anterior and posterior slopes of the dissoconch are concave, so that the prodissoconch appears to be sitting on a neck. The shell is also more equilateral than in *C. projecta*.

Etymology

Named after Mr Jim Beck in appreciation of the years of sorting assistance he has provided in Malacology at the Australian Museum.

Condyllocuna tricola n. sp.

(Figs 19, 23a–h)

Material examined

Holotype. C388198 (Fig. 23a, d) (1pr) W side Heron Is., Capricorn Group, Great Barrier Reef, Queensland, 23°26'S 151°57'E, tidemark, coll. J. Voorwinde, 1950–1960.

Paratypes. C380338 (Fig. 23*b, e-g*) (5v, 2 embryonic valves), QMMO68918 (Fig. 23*c, h*) (1v), W side Heron Is., Capricorn Group, Great Barrier Reef, Queensland, 23°26'S 151°57'E, tidemark, coll. J. Voorwinde, 1950–1960.

Other material examined. **New South Wales.** Off Ballina, 29°10'S 153°47'E, 103 m, 21 Feb. 1972, C366869 (1v). *Sydney area:* Balmoral Beach, 33°49.7'S 151°15.03'E, 1957, C366959 (1v); Maroubra Bay, 33°57'S 151°15.4'E, 8 July 1919, C380339 (1pr). Bermagui, New South Wales, 36°25'S 150°5'E, 1967, C380332 (1v). **South Australia.** Fisherman Point, Cape Donnington, 34°45.5'S 135°59'E, coralline turf on sheltered intertidal rocks, 14 Feb. 1985, C380337 (7v).

Description

Shell. Maximum length 0.88 mm, maximum height 0.8 mm, equilateral, orthogyrate, translucent or opaque white. Inflation ratio, 1.58–1.70.

Prodissoconch. Maximum length 400 μ m, consisting of prodissoconch I and II. Prodissoconch I with three radiating indentations prodissoconch II smooth with sharp rim.

Dissoconch. Lunule and escutcheon long and broad, with remnants of commarginal ribs. Outline slightly triangular, anterior end extended and rounded distally, posterior end shorter and slightly angled. Exterior sculpture of up to 24 commarginal ribs. Inner margin smooth. Hinge plate not apparent. Two smooth lateral teeth in each valve. Right and left valves anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half length of dorsal slopes. Right valve anterior cardinal tooth (CA3) prominent. Posterior cardinal tooth (CP2) prominent. Posterior cardinal teeth in right valve and anterior cardinal teeth in left valve undeveloped. Internal ligament 50 μ m long, rounded, in resilium.

Dimensions. See Table 14.

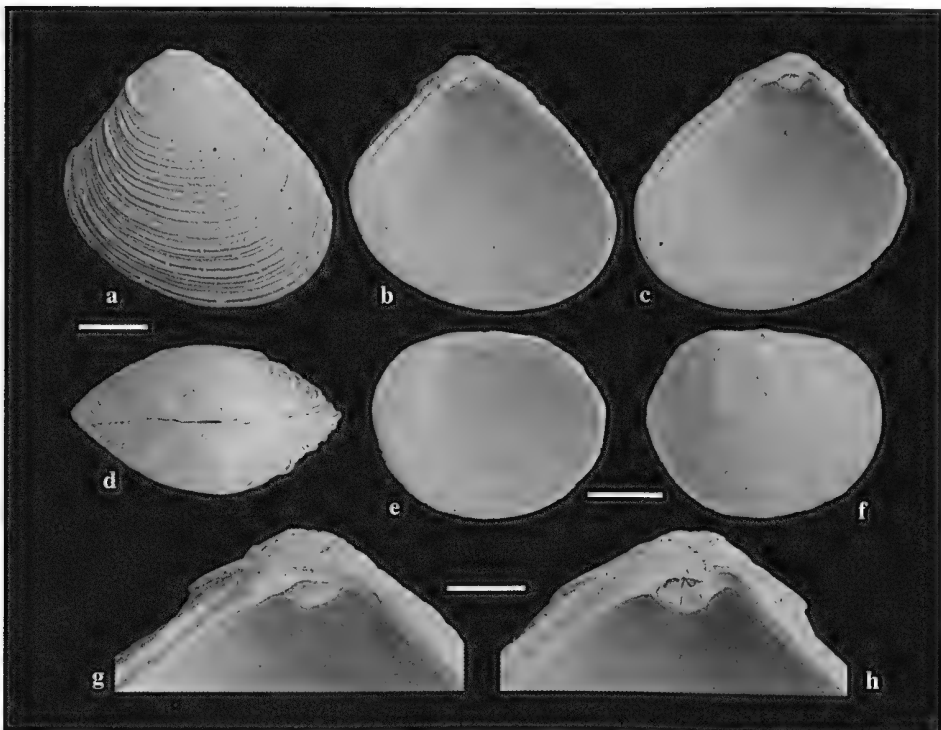


Fig. 23. *Condyllocuna tricola*. a, d, Holotype C388198. b, e-g, Paratypes C380338. a, d, and b, g and c, h, same valves. c, h, Paratype QMMO68918. All Heron Is., Queensland. Scale bars: a-d, 200 μ m; e, f and g, h, 100 μ m.

Table 14. Measurements of specimens of *Condyllocuna tricos*a n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condyllocuna tricos</i> a, holotype, C388198 (Fig. 23a)	0.78	0.74	0.32	0.24	1.63
<i>Condyllocuna tricos</i> a, paratypes, C380338	0.77	0.73	0.29	0.23	1.67
	0.88	0.80	0.40	0.27	1.63
	0.79	0.75	0.38	0.25	1.58
	0.78	0.78	0.34	0.23	1.70

Reproduction

One ready-to-emerge embryo found in a dry specimen (C380320, fig. 23e, f).

Distribution

*Condyllocuna tricos*a has been recorded from Queensland, New South Wales and South Australia. Shells are recorded from intertidal and subtidal to 103 m depth. Found in coralline turf or in sand. This species is only known from shells.

Remarks

This species is congeneric and closely similar to '*Rochefortia*' *io* Bartsch, 1915 (p. 201, pl. 39, fig. 5; pl. 53, figs 5, 6; USNM 251043, syntypes (2 left valves, 1 right valve and 1 pair), Port Alfred, Cape Colony, South Africa. Note that *Condyllocardia io* Bartsch, 1915 (p. 193, USNM 251066, 2 right valves, Port Alfred, Cape Colony, South Africa) is a different taxon, possibly a species of *Benthocardiella*. The lack of well-developed hinge teeth, general outline, commarginal ribbing and radiating indentations of prodissoconch I in *Condyllocuna io* seem very similar to *C. tricos*a, but *C. io* is more posteriorly truncated, anteriorly elongated and has a yellow tinge. As well as the morphological differences mentioned, genetic exchange between the two species seems unlikely because of their highly disjunct distributions and the viviparous mode of reproduction in *C. io*.

Two records of similar looking species need further investigation. Two valves from Bairiki Island, Tarawa Atoll, 1°20'N 172°58'E (C380336) are congeneric and quite similar to the species described herein. Four valves and a whole specimen of an undescribed species from Waiwera, Northland, New Zealand (USNM 680015) are also congeneric and closely similar to *C. tricos*a.

While the Holocene record of one valve from Lake Baghdad, Rottneest Island, Western Australia (C380335) may indicate a larger area of distribution in the Holocene than today, it is equally likely that this record is based on a very similar taxon. Clearly, more material is required to resolve the distribution of the taxon.

The few collections and patchy distribution may be due to specimens being misplaced in collections because it is difficult to assign to a family without SEM images and can easily be misidentified as a juvenile bivalve because of the lack of elaborate hinge teeth.

Etymology

From '*tricos*' meaning 'full of difficulties, perplexities or tricks', in relation to the difficulties faced in systematic placement of the species.

Genus *Cunanax* Iredale, 1936

Cunanax Iredale, 1936: 272. Type species (original designation): *Cuna pisum* Hedley, 1908.

Diagnosis

Prodissoconch large, non-pelagic type, with a knobbly or pitted prodissoconch I. Prodissoconch II smooth with slight radial structure. Dissoconch with faint radials and commarginal growth lines. Inner ventral margin denticulate. Wide hinge plate with short to very long cardinals. Posterior cardinal CP3 is divided into the cardinal elements CP3a,b. Left valve anterior cardinal CA2 absent, anterior cardinal CA4 dorsally divided into CA4a,b. Left valve posterior cardinals consisting of CP2 and CP4.

Remarks

The inclusion of three additional species, besides the type species, in this genus relies strongly on the prodissoconch and, to a certain extent, cardinal hinge teeth. The prodissoconch is large in *Cunanax*, reflecting a brooding and non-pelagic mode of development, and is sculptured with a central, raised, knobby nucleus and a few non-coherent commarginal structures. This prodissoconch type is not found in any other genus of condylocardiine.

The hinge teeth are generally very large and quite similar to those of the much smaller *Austrocardiella* and *Isodontocardia*, though these two genera have very distinctly different prodissoconchs.

Cunanax pisum (Hedley, 1908)

(Figs 24a–i, 27)

Cuna pisum Hedley, 1908: 476, pl. IX, figs 26, 2 (type locality: off Green Point, Watsons Bay, Sydney Harbour, New South Wales. 33°50.5'S, 151°16.5'E. 15 m, 1873, coll. J. Brazier, pres. C. Hedley, 1908. Holotype (Fig. 24a, b) C029114, 1 complete specimen). – Hedley, 1918: M.16.

Cunanax pisum (Hedley, 1908). Laseyron, 1953: 37, figs 8–8b. – Iredale & McMichael, 1962: 17; Lamprell & Healy, 1998: 170, fig. 487.

Condylocuna moringa Laseyron, 1953: 40, figs 18, 18a (type locality: off North Head, Sydney, New South Wales. 33°50'S, 151°18'E. 27 m, pre 1950, coll. C. F. Laseyron. Holotype (Fig. 24c, d) C090555 (2v from very likely one specimen)). – Iredale & McMichael, 1962: 17; Lamprell & Healy, 1998: 170, fig. 483.

Other material examined. **Queensland.** Off S end Fraser Is., 25°48'S 153°46'E, 73 m, soft corals, 10 Nov. 1976, C381216 (1v). NNE of Cape Moreton, 26°52.5'S 153°36'E, 183 m, 1967, C381214 (7v). NE of Cape Moreton light, 26°55.5'S 153°33.5'E, 115–119 m, 1968, C366547 (1v). NE of Cape Moreton, 26°55.5'S 153°33.5'E, 115–124 m, 1967, C379868 (12v), and 27°S 153°35'E, 128–183 m, 1967, C381212 (14v). Off S end Fraser Is., 27°57.13'S 153°51.05'E, 201 m, sand, shell, brachiopods and bryozoans, 10 Nov. 1976, C381215 (23v). **New South Wales.** Off Tweed Heads, 28°17'S 153°44'E, 73 m, coarse sand and 'beach rock', 9 Nov. 1976, C366516 (2v). Off Ballina, 29°10.2'S 153°43.7'E, 86 m, 22 Feb. 1972, C366539 (2v). N of Coffs Harbour, 29°39.1'S 153°41.7'E, 95 m, 22 Feb. 1972, C366515 (1pr). 12 km E of Cakora Point, S of Yamba, 29°39.8'S 153°26.4'E, 55 m, 22 Feb. 1972, C366517 (17v). N of Coffs Harbour, 29°39.8'S 153°37.4'E, 82 m, 22 Feb. 1972, C366544 (12v), and 29°40.3'S 153°30.4'E, 71 m, 22 Feb. 1972, C381218 (1v). 15 km NE of Coffs Harbour, 30°15'S 153°19'E, 73–82 m, 1967, C366552 (2v). NE of Port Macquarie, 31°23'S 153°12'E, 183 m, 14 Oct. 1913, C37786 (3v). Port Stephens, 32°42'S 152°5'E, 1888, C47623 (1pr). Off Nelson Bay, Port Stephens, 32°43'S 152°15'E, 46–78 m, 1967, C366553 (2v). North Fingal Bay, near Port Stephens, 32°44.75'S 152°10.5'E, 1950, C366548 (2v). Off Newcastle, 33°2.2'S 152°23.7'E, 148 m, 3 March 1972, C381220 (5v). Off Tuggerah Lake, 33°20'S 151°39.4'E, 60 m, 11 March 1972, C366541 (2v). **Sydney area:** Collaroy Beach, 33°43.7'S 151°18'E, shell sand, 1950, C366549 (6v); S end of Collaroy Beach, 33°44'S 151°18'E, Aug. 1971, C366844 (1v); off Long Reef, 33°45'S 151°19'E, 26 m, 1950, C366540 (29v); off Chinamans Beach, 33°48.97'S 151°14.87'E, 3.5–7.5 m, 1967, C366264 (17v);

between Grotto and Dobroyd Pts, 275 m off Washaway Beach, 33°49'S 151°16'E, 14.5–18 m, 9 March 1969, C366545 (20+v); 33°49.5'S 151°21.6'E, 64–66 m, 27 Feb. 1973, C366513 (4v); off Balmoral, 33°49.5'S 151°15.4'E, 3.5–9 m, 1950, C381221 (7v); 33°50'S 151°18'E, 27 m, 1953, C315599 (19v); 33°51'S 151°15'E, 1900, C47622 (4v). Ulladulla, 35°21.5'S 150°28.5'E, in beach shell sand, 1950, C366543 (2v). **South Australia.** SE of Kangaroo Is., 37°10'S 138°30'E, 155 m, 26 June, 1962, C381217 (6v).

Description

Shell. Maximum length 6.33 mm, maximum height 6.65 mm, inequilateral, with umbo slightly displaced from middle, orthogyrate and white to bone coloured. Inflation ratio, 1.23–1.64.

Prodissoconch. Maximum length 1270 μ m, consisting of prodissoconch I and II. Prodissoconch I pitted, prodissoconch II with slight radial pattern and sharp rim.

Dissoconch. Lunule and escutcheon long and broad with commarginal sculpture. Outline oval to triangular, with anterior end extended and broadly rounded, posterior end narrowly rounded, dorsal slopes straight or slightly concave. External sculpture of up to 36 sculpture raised commarginal ribs and 18–21 faint radial ribs. Inner margin denticulate with

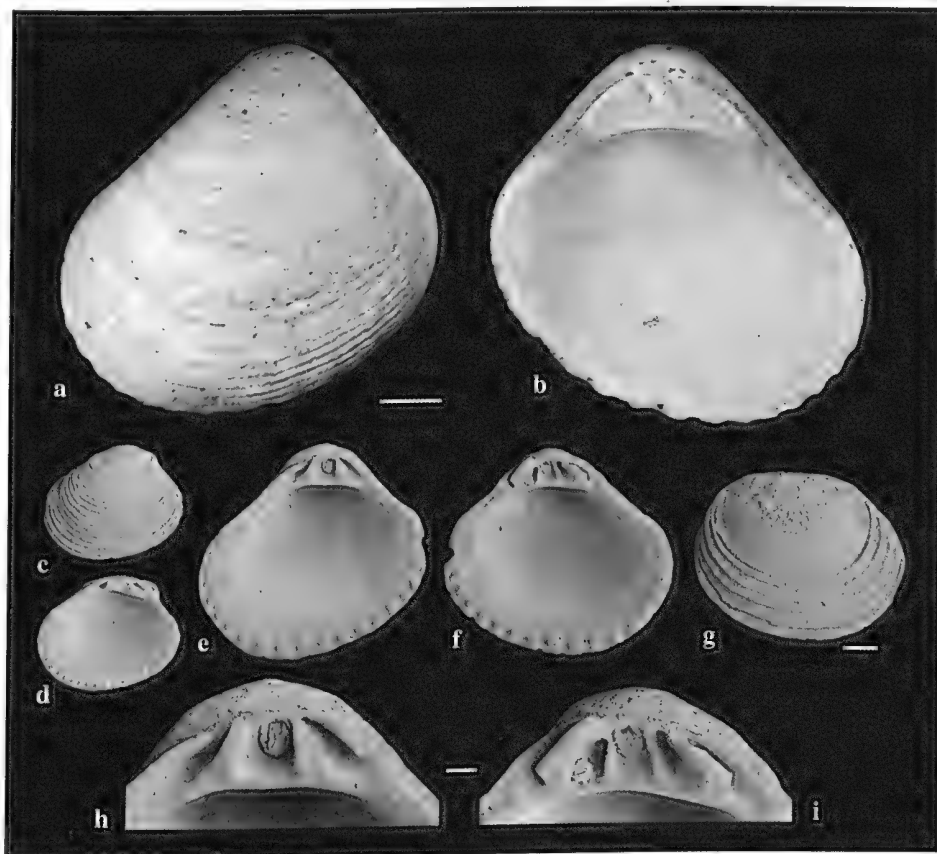


Fig. 24. *Cunanax pisum*. a, b, *Cuna pisum* holotype C029114, off Green Point, Sydney Harbour, New South Wales. c, d, *Condyllocuna moringa* holotype, C090555, off North Head, Sydney, New South Wales. e, f and h, i, C366544, Sow and Pigs Reef, New South Wales. g, C366264, Sydney Harbour, New South Wales. e, h and f, i, same valves. Scale bars: a–f, 1 mm; h, i, 200 μ m.

18–21 denticles. Hinge plate wide and long. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half the length of the dorsal slopes. Right valve anterior cardinal tooth (CA3) triangular and oblique. Posterior cardinal tooth (CP3) divided into small and marginal element CP3a and triangular and ventrally directed CP3b. Left valve anterior cardinal tooth (CA4) divided into dorsally interconnected large squat, marginal CA4a and slender, marginally directed CA4b. Posterior cardinal teeth (CP2, CP4) present and dorsally connected, CP2 being the largest, squat and marginally placed and CP4 being slender and ventrally directed. Internal ligament 200 μ m long, rounded, in resilium.

Dimensions. See Table 15.

Distribution

From Fraser Island, Queensland, south to Ulladulla. The single record from South Australia is likely to be a locality error. Shells have been found from 4–201 m depth, in sand, shell sand and rubble, bryozoan sediment and among soft coral. This species is only known from shells.

Remarks

Laseron (1953) remarked that neither Hedley (1902), in describing this species, nor Iredale (1936), when including this species in *Cunanax*, actually commented on the hinge. Laseron (1953) further noted after examining the hinge that this species is probably not related to any of the recent condylocardiines.

The species *Condylocuna moringa* is based on a juvenile of *Cunanax pisum* and thus a synonym.

Bernard (1897a: p. 196) mentioned the primitive characters of the hinge of *Condylocardia*, which he considered of intermediate form between anisomyarian isodonts (Spondylidae) and heterodonts. The hinge of *C. pisum* could be considered even more plesiomorphic.

Table 15. Measurements of specimens of *Cunanax pisum* (Hedley, 1908)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI \times 2
<i>Cuna pisum</i> , holotype, C029114 (Fig. 24a, b)	6.06	5.63	1.27	2.11	1.44
<i>Condylocuna moringa</i> , holotype, C090555 (Fig. 24c, d)	2.23	1.81	0.99	0.68	1.64
<i>Cunanax pisum</i> , C381217	4.90	4.84	1.01	1.77	1.38
	4.85	4.66	1.16	1.79	1.35
	6.33	6.24	1.27	2.22	1.43
	6.50	6.65	1.23	2.64	1.23
	4.02	3.66	1.04	1.33	1.51

Cunanax compressa (Hedley & May, 1908)

(Figs 25a–g, 27)

Cuna compressa Hedley & May, 1908: 124, pl. 24, figs 29–32 (type locality: off Cape Pillar, Tasmania, 43°13'S, 148°5'E. 183 m. 17–18 Dec. 1907. Lectotype (here selected) (Fig. 25a) C029080, (1v), paralectotypes C170793 (20+v)).

Condylocardia compressa (Hedley & May, 1908). Verco, 1908a: 359. – May 1921: 17; May, 1923: pl. 7, fig. 8; Kershaw, 1955: 296.

Volupicuna compressa (Hedley & May, 1908). Lamprell & Healy, 1998: 176, fig. 516.

Other material examined. **Tasmania.** Off Cape Naturaliste, 40°49.5'S 148°32.1'E, 62 m, yellow-orange coarse mud-sand, 26 March 1973, C378452 (1v), and 40°50.6'S 148°46.5'E, 399 m, silty sand and bryozoa, 26 March 1973, C378451 (7v). NE of Cape Pillar, 43°10'S 148°6.7'E, 113 m, medium sand and bryozoa, 13 March 1973, C378453 (1v), and 43°10'S 148°12'E, 172 m, fine-medium sand and bryozoa, 13 March 1973, C378454 (2v). 15 km NE of Tasman Is., 43°12.5'S 148°13.75'E, 570.5 m, 24 March 1970, C378464 (1v). 3 km S Tasman Head, S Bruny Is., 43°33.75'S 147°19.35'E, 73 m, 24 March 1970, C378471 (48v). S of Storm Bay, 43°35.5'S 147°32.3'E, 121 m, 30 March 1973, C378465 (7v). S of South East Cape, 43°42.2'S 146°18.6'E, 108 m, 4 April 1973, C378450 (8v). Between South East and South West Capes, 43°58.5'S 146°19.1'E, 168 m, 4 April 1973, C378473 (1v). S of D'Entrecasteaux Channel, 44°2.9'S 147°10'E, 168 m, 1 April 1973, C378472 (2v). SW of Low Rocky Point, 43°6.4'S 145°16.1'E, 154 m, 10 April 1973, C378457 (2v). SW of Low Rocky Point, 42°58.2'S 145°26.6'E, 84 m, 10 April 1973, C378458 (5v). SW of Low Rocky Point, 42°58.2'S 145°5'E, 188 m, 10 April 1973, C378456 (5v). NW of Low Rocky Point, 42°51.2'S 145°0.6'E, 146 m, 11 April 1973, C378459 (1v). S of Macquarie Hbr, 42°30'S 145°9.1'E, 88 m, 11 April 1973, C378470 (1v). SW of Sandy Cape, 41°39.5'S 144°37.1'E, 130 m, 15 April 1973, C378467 (7v). W of Sandy Cape, 41°29.5'S 144°24.4'E, 119 m, 15 April 1973, C379866 (15v). NW of Sandy Cape, 41°9.4'S 144°10.6'E, 132 m, 14 April 1973, C378469 (6v, 1pr). S of West Point, 41°9.2'S 144°24.2'E, 88 m, 14 April 1973, C378460 (8v). W of West Point, 41°1.2'S 144°21.5'E, 80 m, 14 April 1973, C378461 (3v). W of West Point, 41°S 143°55'E, 170 m, 14 April 1973, C378463 (3v). W of West Point, 41°S 144°7.5'E, 104 m, 14 April 1973, C378462 (3v). Bass Strait, E of Grassy, King Is., 40°11'S 144°39'E, 58 m, 23 June 1962, C378447 (2v). E of King Is., Bass Strait, 40°0.1' 144°13.7'E, 33 m, 30 April 1973, C378455 (6v).

Description

Shell. Maximum length 9.01 mm, maximum height 8.91 mm, inequilateral, with umbo slightly displaced from middle, orthogyrate and white. Inflation ratio, 1.67–2.42.

Prodissoconch. Maximum length 1.38 mm, consisting of prodissoconch I and II. Prodissoconch I pitted, prodissoconch II with slight radial pattern and sharp rim.

Dissoconch. Lunule and escutcheon short and narrow, with commarginal pattern. Outline triangular, anterior end extended and broadly rounded, posterior end short and narrowly rounded. External sculpture of commarginal growth lines and 20–24 faint radial ribs. Inner margin denticulate with 20–24 denticles. Hinge plate very wide. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half length of dorsal slopes. Right valve anterior cardinal tooth (CA3) oblique, pointing anteriorly, longitudinally split into small segments. Posterior cardinal tooth (CP3) divided into large ventrally directed CP3a and marginal CP3b. Left valve anterior cardinal tooth (CA4) divided into narrow anterior marginal element CA4a and larger oblique CA4b. Posterior cardinal teeth CP2 and CP4 present, both dorsally connected, CP2 largest and marginally placed. Internal ligament 450 µm long, triangular, in resilium.

Dimensions. See Table 16.

Distribution

Tasmania. 33–570 m depth. Found in sand, mud or bryozoan substrate. This species is only known from shells.

Remarks

Cunanax compressa is hard to separate from *Cunanax crassidentata* but the smaller hinge plate, less dorsoventrally directed cardinals, larger prodissoconch (1.12 ± 0.14 mm versus 0.91 ± 0.18 mm in *C. crassidentata*; $X \pm SD$, $n=6$ in *C. compressa* and $n=5$ in *C. crassidentata*, t -test, $p<0.01$), more numerous radial ribs and the general shape are useful characters.

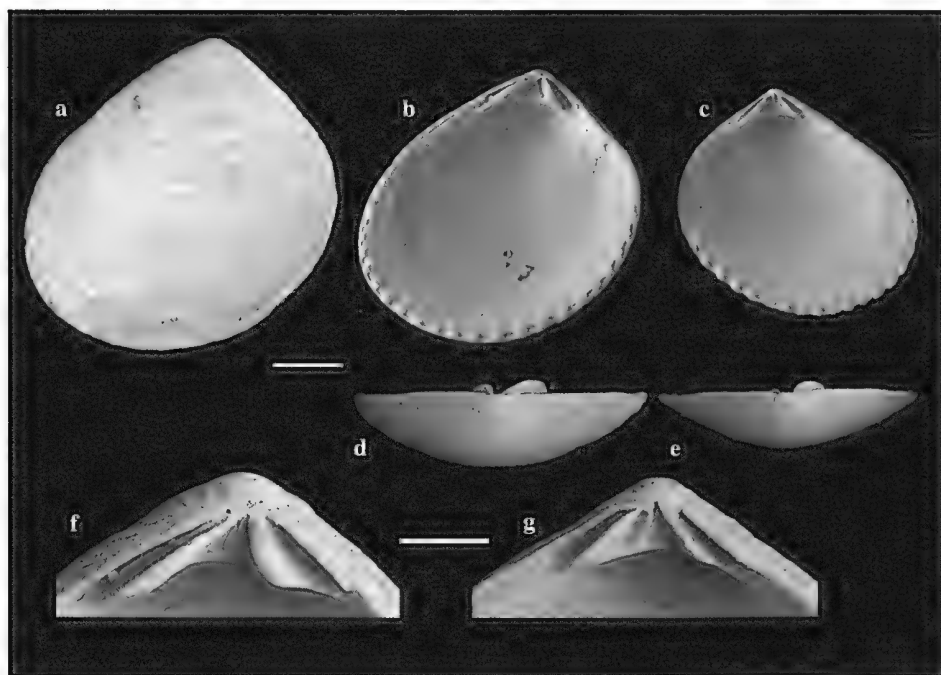


Fig. 25. *Cunanax compressa*. a, *Cuna compressa* lectotype C029080, off Cape Pillar, Tasmania. b–g, C378471, Tasman Head, Tasmania. Scale bars: a–e, 200 μ m; f, g, 100 μ m.

Table 16. Measurements of specimens of *Cunanax compressa* (Hedley & May, 1908)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI \times 2
<i>Cuna compressa</i> , lectotype, C029080 (Fig. 25a)	9.01	8.91	1.00	2.56	1.76
<i>Cunanax compressa</i> , paralectotypes, C170793	8.00	8.10	1.10	2.14	1.87
	8.42	8.22	1.38	2.52	1.67
	7.98	7.14	1.14	1.78	2.24
	7.12	6.48	1.00	1.58	2.25
	5.70	4.96	1.08	1.18	2.42

Cunanax crassidentata (Cotton, 1930)

(Figs 26a–g, 27)

Condylocardia crassidentata Cotton, 1930: 236, fig. 9 (type locality: Beachport, South Australia, 73 m. Holotype (Fig. 26a, b) SAMA D.10110). – Cotton, 1961: 204, fig. 204; Lamprell & Healy, 1998: 168, fig. 474.

Other material examined. **Tasmania.** Bass Strait, E of Grassy, King Is., 40°11'S 144°39'E, 58 m, 23 June 1962, C379865 (3v). **South Australia.** Off Beachport, 37°29'S 140°E, 73 m, 1909, C25985 (5v) and C25986 (4v); 64 km S of Cape Wiles, 35°39'S 136°40'E, 174–183 m, 28 Aug. 1909, C32086 (24v).

Description

Shell. Maximum length 6.95 mm, height 7.57 mm, inequilateral, with umbo equidistant from centre and end of shell, opisthogyrate and white. Inflation ratio, 1.51–2.23.

Prodissoconch. Maximum length 1.13 mm long, consisting of prodissoconch I and II. Prodissoconch I pitted, prodissoconch II with slight radial pattern and sharp rim.

Dissoconch. Lunule and escutcheon short, narrow and smooth. Outline triangular, with anterior end extended and broadly rounded, posterior end shorter and narrowly rounded. External sculpture of commarginal growth lines and up to 21 faint radial ribs. Inner margin denticulate with 24 denticles. Hinge plate very wide. Right valve anterior cardinal tooth (CA3) weakly bifid, and directed obliquely anterior. Posterior cardinal tooth (CP3) divided into slender marginal CP3a and ventrally directed CP3b. Left valve anterior cardinal tooth (CA4) divided into marginal and narrow CA4a and more ventrally directed CA4b. Posterior cardinal teeth (CP2 and CP4) present, CP4 very small. Internal ligament about 30 μ m, triangular, in resilium.

Dimensions. See Table 17.

Distribution

South Australia and north western Tasmania, 58–183 m depth. Habitat unknown. This species is only known from shells.

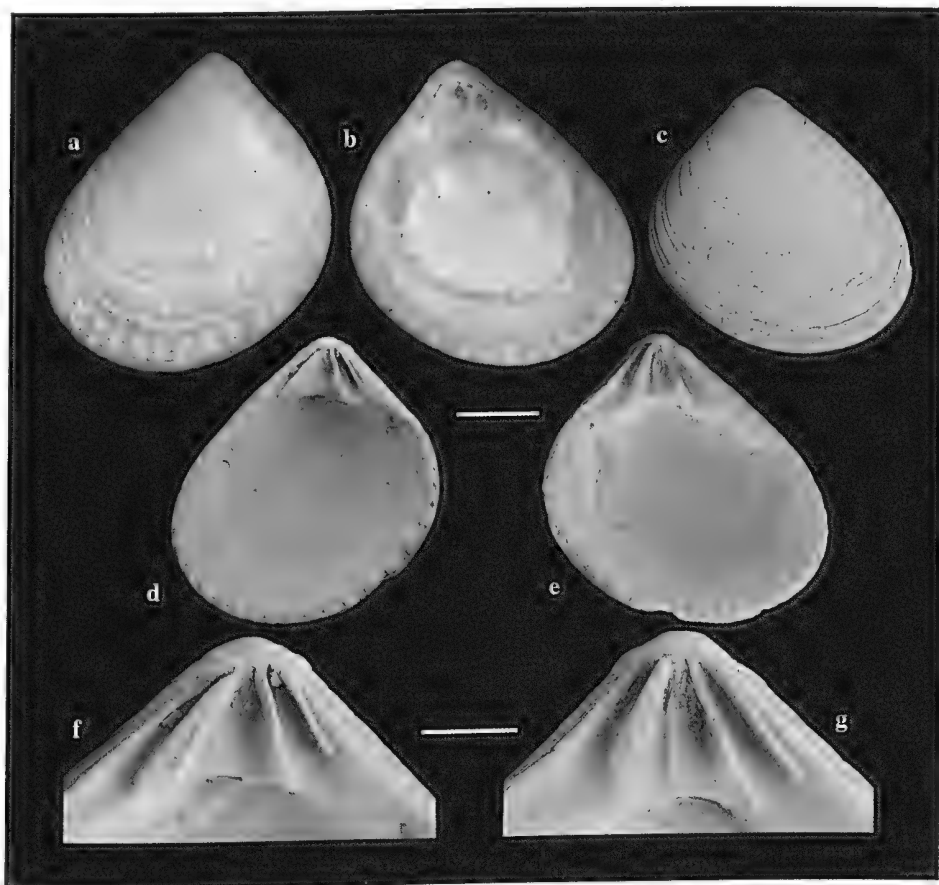


Fig. 26. *Cunanax crassidentata*. a, b, *Condylocardia crassidentata* holotype SAMA D.10110, Beachport, South Australia. c–g, C025985, off Beachport, South Australia. d, f and c, g same valves. Scale bars: a–e, 2 mm; f, g, 1 mm.

Table 17. Measurements of specimens of *Cunanax crassidentata* (Cotton, 1930)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Condylocardia crassidentata</i> , holotype, SAMA D.10110 (Fig. 26a, b)	6.95	7.57	1.08	2.30	1.51
<i>Cunanax crassidentata</i> , C025985	6.38	6.92	0.71	1.66	1.92
	5.87	6.14	0.76	1.50	1.96
	6.34	6.60	0.92	1.42	2.23
	6.19	6.40	1.13	1.55	2.00
	5.63	5.46	1.05	1.40	2.01

Remarks

Cunanax crassidentata has characters that appear intermediate between *C. compressa* and *C. subradiata*. Externally, some specimens resemble large *C. subradiata*, but the large hinge teeth and hinge plate clearly set it apart. See Remarks under *C. compressa* for separation from *C. crassidentata* and *C. compressa*.

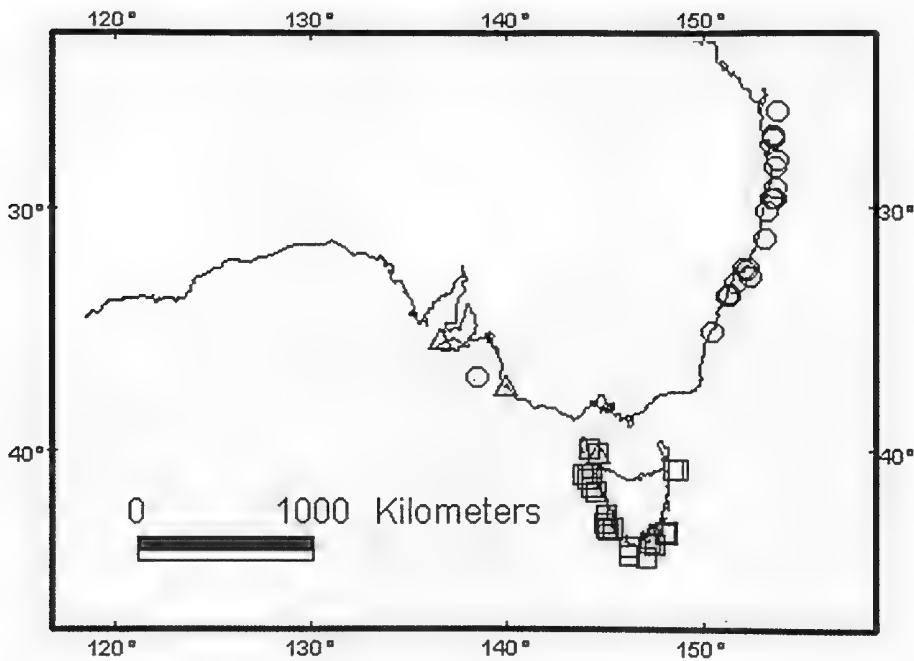


Fig. 27. Distribution of *Cunanax compressa* (□), *C. crassidentata* (Δ) and *C. pisum* (○).

Cunanax subradiata (Tate, 1889)

(Figs 28a–n, 29)

Carditella subradiata Tate, 1889: 62, pl. 11, fig. 7 (type locality: Royston Head, South Australia, in shell sand. Holotype (Fig. 28c) (1v) SAMA D.12919).

Condylocardia porrecta Hedley, 1906b: 475, pl. 38, fig. 24 (type locality: dredged off Masthead Island, Capricorn Group, Great Barrier Reef, Queensland, 23°32'S, 151°45'E. 31–37 m. 25–29 Oct. 1904,

coll. and pres. C. Hedley. Lectotype (here selected) (Fig. 28*d*) (1v) C019659, paralectotypes (including Fig. 28*e*, *f*) (12pr, 48v), C388167. There are more paralectotypes in the Tomlin Collection, National Museum of Wales, Cardiff (Oliver, 1982)). – Verco, 1908*a*: 360; Gatliff & Gabriel, 1910: 97; Hedley, 1918: M.17; May, 1921: 17; May, 1923: pl. 7, fig. 11; Macpherson & Chapple, 1951: 149; Lamprell & Healy, 1998: 172, fig. 493.

Condylocardia subradiata (Tate, 1889). Verco, 1908*a*: 358, pl. xvii, figs 25–28. – Gatliff & Gabriel, 1922: 160; Macpherson & Chapple: 1951: 149; Cotton, 1961: 204, fig. 206; Lamprell & Healy, 1998: 168, fig. 477.

Radiocondyla ampla Laseron, 1953: 42: fig. 22 (type locality: dredged off Long Reef, Collaroy, Sydney, New South Wales, 33°45'S, 151°19'E, pre 1948. Lectotype (here selected) (Fig. 28*a*) (1v) C090560, paralectotype, (1pr), C388170). – Iredale & McMichael, 1962: 17; Lamprell & Healy, 1998: 172, fig. 495.

Radiocondyla rotunda Laseron, 1953: 42, fig. 9 (type locality, off Crookhaven, New South Wales. 34°55'S, 150°54'E. 55–64 m, pre 1948, coll. C. F. Laseron. Holotype (Fig. 28*b*) (1v) C090561). – Iredale & McMichael, 1962: 17; Lamprell & Healy, 1998: 172, fig. 496.

Radiocondyla subradiata (Tate, 1889). Macpherson & Gabriel, 1962: 321.

Radiocondyla porrecta (Hedley, 1906*b*). Macpherson & Gabriel, 1962: 321. – Lamprell & Healy, 1998: 172, fig. 493.

Other material examined. **Queensland.** *Great Barrier Reef:* Euston Reef, SW side, 16°40'S 146°13'E, 21 m, at bottom of sand slope below steep coral walls, 30 Nov. 1972, C379238 (13v); Swain Reefs, 3 km NE of W side of Bylund (Gillett) Cay, 21°42'S 152°26'E, 64–73 m, 17 Oct. 1962, C378488 (20+v), and 21°43'S 152°25'E, 27–37 m, coral rubble, inside reef, 16 Oct. 1962, C379237 (12v); Heron Is., 23°26'S 151°57'E, 36.5 m, Dec. 1956, C378492 (4v), and 2 m, 1959, C378498 (1v); Masthead Is., 23°32'S 151°45'E, 31–37 m, 25 Oct. 1904, C19659 (many v and pr); E of Lady Musgrave Is., 23°50.1'S 152°32.1'E, 132 m, 4 July 1984, C378491 (1v) and 23°51.2'S 152°34.5'E, 175–200 m, 4 July 1984, C378490 (5v). Off Maryborough, 25°47'S 153°33'E, 64 m, 25 Oct. 1970, C378489 (5v). Off S end Fraser Is., 25°48'S 153°46'E, 73 m, soft corals, 10 Nov. 1976, C378493 (1v), and 25°57.9'S 153°34.4'E, 58–60 m, coarse sand and shell, 10 Nov. 1976, C379227 (6v). NE of Cape Moreton, 26°55.5'S 153°33.5'E, 115–119 m, 1968, C378495 (1v), 115–124 m, 1967, C378499 (4v), and 27°S 153°35'E, 128–183 m, 1967, C378494 (3v). **New South Wales.** Off Ballina, 29°10.2'S 153°43.7'E, 86 m, 22 Feb. 1972, C379240 (2v). N of Coffs Harbour, 29°39.8'S 153°37.4'E, 82 m, 22 Feb. 1972, C379239 (11v). 14 km NE of Coffs Harbour, 30°15'S 153°19'E, 73–82 m, 1967, C366846 (1v). Off Port Macquarie, 31°20'S 153°5'E, 77 m, 25 Feb. 1972, C366841 (1v). Off Forster, 32°13.13'S 152°51.1'E, 111 m, 6 Dec. 1957, C366829 (3v). *Sydney area:* 33°43'S 151°46'E, 174 m, 19 Dec. 1985, C379230 (1v); Collaroy Beach, 33°43.7'S 151°18'E, 1950, C366825 (1v); S end of Collaroy Beach, 33°44'S 151°18'E, Aug. 1971, C366834 (2v); Long Reef, 33°44.6'S 151°18.6'E, rocks, 1967, C378496 (2v); off Long Reef, 33°45'S 151°19'E, 26 m, 1948, C90560 (3v); 33°45.4'S 151°21.6'E, 40 m, 29 March 1972, C366848 (1v); 33°46'S 151°43'E, 176 m, 5 Dec. 1977, C379225 (1v); Manly Beach, 33°47.7'S 151°17.19'E, 13 May 1917, C366810 (1pr); off North Head, 33°50'S 151°18'E, 27 m, 1953, C90555 (2v); 33°50'S 151°19'E, 46–73 m, 1967, C378520 (2v); 33°51.3'S 151°14.8'E, 1967, C366849 (1v); 33°55'S 151°25.5'E, 75–150 m, 18 June 1962, C378518 (3v); 33°58'S 151°29'E, 150 m, 18 June 1962, C379244 (3v); c. 30 km E off Little Bay, Malabar, 33°58.8'S 151°34.5'E, 192–203 m, 9 Aug. 1973, C379232 (1v); SW end of Gunnamatta Bay, 34°4.3'S 151°8.7'E, in channel, 1950, C378519 (1pr); S of Port Hacking, 34°9.6'S 151°26.3'E, 205 m, 13 March 1972, C379247 (1v). 8–13 km off Port Kembla, 34°27.9'S 151°4.5'E, 115–137 m, mud and pebbles, 18 March 1898, C13265 (6v). Off Montague Is., Narooma, 36°15'S 150°13'E, 9–16 m, 3 Jan. 1916, C379229 (6v). SE of Montague Is., 36°19.9S 150°16.9'E, 124 m, 31 March 1972, C366845 (1v). Twofold Bay, 37°5'S 149°54'E, 1919, C366850 (1v). 32 km SE of Twofold Bay, 37°26'S 150°15'E, 149 m, 19 June 1962, C379243 (2v). **Victoria.** Off Western Port, 38°40.5'S 144°47.4'E, 75 m, 2 May 1973, C379241 (4v). S of Warrnambool, 38°43'S 142°29'E, 75 m, 24 June 1962, C379242 (1v). Spring Creek, Minhamite, 38°1'S 142°26'E, 26 April 1980, C378512 (2v). **Tasmania.** S of West Point, 41°9.2'S 144°24.2'E, 88 m, 14 April 1973, C378475 (6v). W of West Point, 41°1.2'S 144°21.5'E, 80 m, 14 April 1973, C378487 (1v). 41°S 144°7.5'E, 104 m, 14 April 1973, C378497 (6v). *King Island area:* 40°24.8'S 143°34.3'E, 110 m, 29 April 1973, C378468 (16v). 40°22.5'S 143°39'E, 128 m, 25 April 1973, C378484 (7v). 40°20'S 144°10'E, 58 m, 12 April 1973, C379864 (7v). 40°20'S 144°36.4'E, 55 m, 12 April 1973, C378500 (22v). 40°11'S 144°39'E, 58–77 m, 23 June 1962, C378482 (19v). 40°10.5'S 144°18.6'E, 51 m, 24 April 1973, C378476 (17v). 40°0.1'S 144°13.7'E, 33 m, 30 April 1973, C378486 (1v). 40°S 144°38.5'E, 46 m, 30 April 1973, C378479 (13v). **South Australia.** Off Beachport, 37°29'S 140°E, 73 m, 1909, C25984 (10v), and C30669 (6v). 80 km SE of Kangaroo Is., 37°S 138°33'E, 77 m, 26 June 1962, C379235 (36+v). SE of Kangaroo Is., 37°10'S

138°30'E, 155 m, 26 June 1962, C379236 (55v). 64 km S of Cape Wiles, 35°39'S 136°40'E, 174–183 m, 28 Aug. 1909, C378515 (5v). Nuyts Archipelago, N of St Francis Is., 32°29'S 133°18'E, 20–30 m, Sep. 1974, C379245 (20v). Petrel Bay, N of St Francis Is., 32°29'S 133°18'E, 20–30 m, 28 Dec. 1973, C379248 (13v). Great Australian Bight, 80 km SW of Cape Adieu, 32°42'S 131°27'E, 79 m, 4 July 1962, C379226 (57v). **Western Australia. Great Australian Bight:** 33°5'S 128°40'E, 75 m, 5 July 1962, C378516 (6v); 33°5'S 128°40'E, 75–147 m, 5 July 1962, C379249 (21v); 121 km E of Rocky Point, 33°43'S 125°4'E, 77–80 m, 7 July 1962, C378517 (32v); 34°13'S 125°4'E, 75 m, 8 July 1962, C379863 (7). *Recherche Archipelago:* 34°27.5'S 122°0.3'E, 27 March 1981, C378509 (29v); 34°14'S 121°23'E, 78 m, March 1981, C382747 (1v); E of Hood Point, 34°25'S 121°20'E, 158 m, 9 July 1962, C378972 (45v); 34°2.9'S 121°17.4'E, 82 m, March 1981, C382744 (1v); E of Hood Point, 34°21'S 121°16'E, 79 m, 9 July 1962, C378968 (7v). *Off Esperance:* 34°6.75'S 121°11.55', 85 m, coarse shell sand, Feb. 1981, C382732 (8v); 34°21.6'S 121°9.6'E, 70–90 m, fine sand and shell, Feb. 1981, C382735 (8v); 34°22.9'S 121°3.5'E, 85 m, coarse shell sand, Feb. 1981, C382730 (7v); 34°1.8'S 121°1.8'E, sand, 3 Feb. 1981, C378966 (14v). E of Cheyne Bay, 34°55'S 119°E, 71–76 m, 7 Aug. 1962, C378971 (29v). *Off Albany:* 35°2.4'S 118°50'E, 73 m, sand and broken shell, 21 March 1980, C378973 (2v); 35°6'S 118°39'E, 76 m, sand and broken shell, 20 March 1980, C378974 (7v); 35°14.8'S 118°30'E, 124 m, sand, 20 March 1980, C378970 (17v); 35°14.4'S 118°20.5'E, 75 m, sand and shell, 12 March 1980, C378501 (5v); 35°20'S 118°20'E, 112 m, sand and shell, 12 March 1980, C378969 (18v); 35°14.7'S 118°10.4'E, 71 m, 12 March 1980, C378502 (9v). *Off Rottnest Island:* 31°45'S 115°16.4'E, 93 m, 12 Nov. 1980, C378504 (12v); 31°43.1'S 115°15'E, 100 m, broken shell and coral, Jan. 1981, C378513 (20v); 31°41.1'S 115°14'E, 98 m, broken shell and coral, Jan. 1981, C378511 (5v); Stn 61, 31°43.4'S 115°13.8'E, 120 m, 12 Nov. 1980, C382736 (13v); Stn 62, 31°43.4'S 115°13.8'E, 120 m, 12 Nov. 1980, C382738 (1v); 31°42.2'S 115°13.6'E, 105 m, 12 Nov. 1980, C382729 (8v); 31°37.8'S 115°10.7'E, 110 m, fine sand and broken shell, Jan. 1981, C378510 (5v); 31°39'S 115°10'E, 124 m, fine sand and broken shell, Jan. 1981, C382737 (1v); 31°40.6'S 115°9.6'E, 100 m, 12 Nov. 1980, C378979 (14v); 31°45'S 115°9'E, 144–150 m, 18 March 1972, C382745 (1v). SW of Mandurah, 32°43'S 114°48'E, 192–179 m, C382741 (1v). S of Cape Leeuwin, 34°25'S 114°40'E, 73–144 m, 9 Aug. 1962, C378976 (2v). NW of Green Head, 30°37'S 114°38'E, 128–140 m, 22 March 1972, C378507 (2v). NW of Cervantes, 30°30'S 114°38'E, 256–192 m, 22 March 1972, C378977 (4v). W of Jurien Bay, 30°14'S 114°35'E, 146–151 m, 19 March 1972, C378506 (3v). NW of Green Head, 29°58'S 114°27'E, 197–219 m, 22 March 1972, C378508 (3v). NW of Green Head, 29°59'S 114°25'E, 150 m, 22 March 1972, C378967 (2v). NW of Beagle Is., 29°43.5'S 114°20'E, 183 m, 19 March 1972, C378503 (6v). Off Dongara, 29°33'S 114°19.5'E, 152–157 m, 19 March 1972, C378505 (2v). W of Cliff Head, 29°34.1'S 114°17.4'E, 126 m, 18 Feb. 1976, C378978 (4v). NW of Beagle Is., 29°43'S 114°17'E, 274–283 m, 20 March 1972, C378975 (3v). 32 km W of Dongara, 29°6.7'S 114°E, 91 m, 19 Feb. 1976, C382733 (2v). W of Dongara, 29°7.5'S 113°57.4'E, 110 m, sponges and stone rubble, 19 Feb. 1976, C382734 (13v).

Description

Shell. Maximum length 4.43 mm, maximum height 4.4 mm, inequilateral, with umbo slightly displaced from middle, orthogyrate and white to cream in colour. Inflation ratio, 1.18–1.92.

Prodissoconch. Maximum length 820 µm, consisting of prodissoconch I and II. Prodissoconch I with knobs and two commarginal rib structures, largest forming discontinuity between prodissoconch I and II. Prodissoconch with faint radial pattern and sharp rim.

Dissoconch. Lunule and escutcheon short, narrow, smooth. Outline oval, to triangular with anterior end slightly extended, anterior and posterior end broadly rounded. External sculpture of commarginal growth lines and 12–16 strong radial ribs. Inner margin denticulate with 12–16 denticles. Hinge plate short and narrow. Two smooth lateral teeth in each valve. Right and left valve anterior lateral teeth (LAI, LAII) and posterior lateral teeth (LPIII, LPII) longer than half the length of the dorsal slopes. Right valve anterior cardinal tooth (CA3) narrow and oblique. Posterior cardinal tooth (CP3) arched, divided into cardinal elements CP3a,b. Left valve anterior cardinal tooth (CA4) arched, divided into CA4a,b. Posterior cardinal teeth (CP2 and CP4) present, CP4 vestigial. Internal ligament 175 µm long, rounded, in resilium.



Fig. 28. *Cunanax subradiata*. *a*, *Radiocondyla ampla* lectotype C090560, off Long Reef, Collaroy, Sydney, New South Wales. *b*, *Radiocondyla rotunda* holotype C090561, off Crookhaven, New South Wales. *c*, *Carditella subradiata* holotype SAMA 12919, Royston Head, South Australia. *d*, *Condylocardia porrecta* lectotype C019659, off Masthead Is., Queensland. *e*, *f*, *C. porrecta* paralectotype C388167, off Masthead Is., Queensland. *g*–*l*, *n*, C379863, Great Australian Bight, Western Australia. *m*, C378488, Great Barrier Reef, Queensland. Scale bars: *a*–*j*, 1 mm; *k*, *l*, 200 μ m; *m*, *n*, 100 μ m.

Dimensions. See Table 18.

Distribution

From Euston Reef, Great Barrier Reef, Queensland, to west of Dongara, Western Australia, including southeastern and northwestern Tasmania; 2–219 m depth. Shells are recorded from fine and coarse sand, coral and stone rubble and shell grit. This species is only known from shells.

Table 18. Measurements of specimens of *Cunanax subradiata* (Tate, 1889)

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI×2
<i>Carditella subradiata</i> , holotype, SAMA D.12919 (Fig. 28c)	3.39	3.74	0.70	1.13	1.50
<i>Condylocardia porrecta</i> , lectotype, C019659 (Fig. 28d)	1.68	1.58	0.55	0.71	1.18
<i>Radiocondyla ampla</i> , lectotype (here selected), C090560 (Fig. 28a)	2.70	2.67	0.74	0.87	1.55
<i>Radiocondyla rotunda</i> , holotype, C090561 (Fig. 28b)	2.30	2.19	0.59	0.72	1.60
<i>Cunanax subradiata</i> , C378488 (northern phenotype)	2.43	2.42	0.55	0.86	1.41
	2.50	2.45	0.57	0.85	1.47
	2.45	2.42	0.59	0.84	1.46
	2.27	2.33	0.58	0.95	1.19
	2.02	2.07	0.54	0.78	1.29
<i>Cunanax subradiata</i> , C025984 (southern phenotype)	4.43	4.40	0.76	1.46	1.52
	4.21	4.09	0.80	1.32	1.59
	4.02	3.74	0.82	1.15	1.75
	3.62	3.36	0.80	0.97	1.87
	3.30	3.26	0.72	0.86	1.92

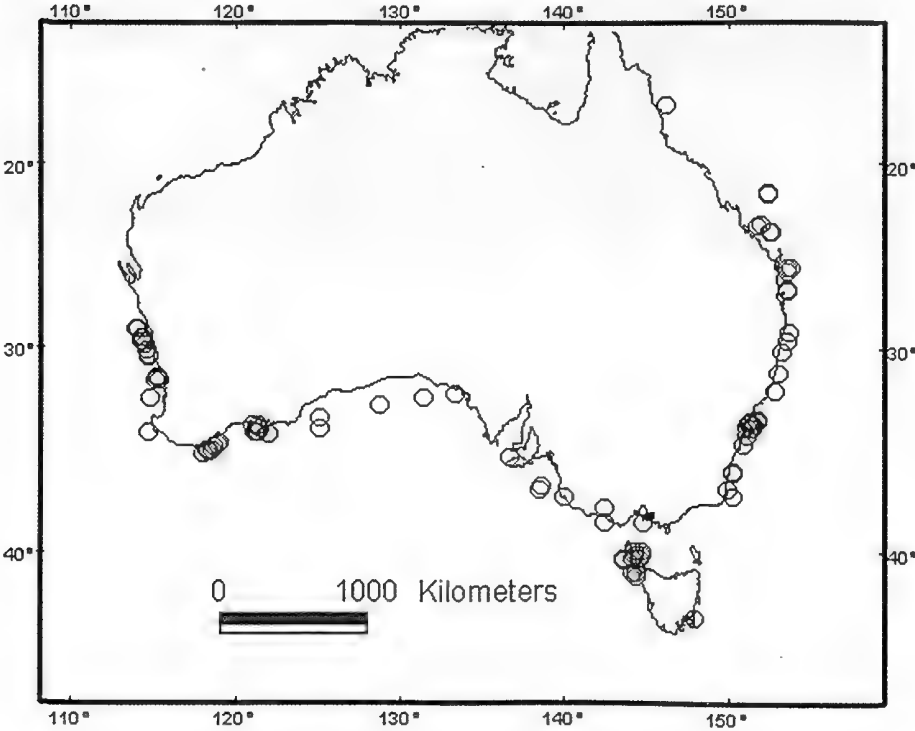


Fig. 29. Distribution of *Cunanax subradiata*.

Remarks

Many references cite *C. subradiata* as having been described in 1888, but Tate's paper was actually published in 1889. Verco (1908a) argued that the reason Tate (1889) included this species in *Carditella* was that he did not observe the hinge teeth and assumed that the posterior part of the shell was elongate. As Verco stated, the hinge teeth clearly place this species with the condyllocardiines and the shell is in fact anteriorly elongate.

The inclusion of *Condyllocardia porrecta* in the synonymy of this taxon is based on the apparent lack of distinguishing characters. Shells from the northern part of the range are smaller and more strongly sculptured, the hinge teeth more spread out and the prodissoconch smaller and (possibly consistently) with nodules not coalescent into commarginal ribs (see Fig. 28m, n). *Condyllocardia porrecta* is not recognised as a separate species or subspecies herein despite the southern-most specimens being easily separated from those from the Great Barrier Reef. Specimens from intermediate localities completely intergrade in terms of shell size, hinge size and general morphology.

As noted under *C. crassidentata*, large specimens of southern *C. subradiata* show some similarities in outline to this taxon. However, as mentioned earlier, the hinge teeth and hinge plate of *C. crassidentata* are larger than those of *C. subradiata*.

Genus *Isodontocardia* n. gen.

Type species: *Isodontocardia microcardia* n. sp.

Diagnosis

External sculpture consisting of scabrous radials and fenestrate interrarial spaces. Hingeplate wide and solid. Right valve hinge elements consist of one anterior cardinal tooth (CA3) and posterior subdivided cardinal (CP3 divided into CP3a,b). Left valve hinge teeth consist of anterior arched and subdivided cardinal (CA4 divided into CA4a,b) and two posterior cardinals (CP2, CP4). Anterior and posterior dorsal slopes dorsally angled and extended beyond lateral teeth. Extended areas sculptured with surface ripples. Prodissoconch consisting of prodissoconch I sculptured with five radial indentations.

Remarks

The type species, *Isodontocardia microcardia*, is distinctly different from any species or genus described. The species has a unique combination of anterior and posterior slope convexity, small prodissoconch and elaborate external radial and commarginal sculpture. The hinge teeth layout resembles that of *Cunanax* and *Austrocardiella* (see Fig. 31). The surface ripples dorsal to the lateral teeth, developed to a lesser extent in some species of *Condyllocardia* (see e.g. *C. notoaustralis* Fig. 6l, m), might assist the cardinal and lateral teeth in locking the valves together. Prodissoconch morphology and the external sculpture suggest a relationship with the Cuninae and Carditidae, whereas the hinge teeth place it firmly in Condyllocardiinae.

Etymology

Iso from Greek, meaning 'equal', *odonto* from Greek for 'tooth' and *cardia* from Greek for 'heart'.

Isodontocardia microcardia n. sp.

(Figs 19, 30a–h)

Material examined

Holotype. (Fig. 30g). C388188, Torres Strait, off Murray Is., 9°56'S 144°4'E, 9–15 m, 30 Aug. 1907, coll. C. Hedley.

Paratypes. C379251 (including Fig. 30h), (5pr, 8v), Torres Strait, off Murray Is., 9°56'S 144°4'E, 9–15 m, 30 Aug. 1907, coll. C. Hedley, C379259, (more than 60v, 3v and 1pr illustrated here, Fig. 30a–f), NTM P14471, (1pr, 4v), Amazon Bay, Milne Bay District, Papua New Guinea, 10°19'S 149°21'E, seaweed dredge, 13 m, 13 Sep. 1948, coll. CSIRO fisheries.

Other material examined. **Northern Territory.** Arafura Sea, c. 72 km N Croker Is., 10°17'S 132°38'E, 65 m, 9 Nov. 1969, C379255 (1v). **Queensland.** Cape York Peninsula, Albany Passage, 10°45'S 142°37'E, 7–26 m, mud and sand, 9 Oct. 1907, C36162 (4v). Gannet Passage, Torres Strait, 10°35'S 141°55'E, 0–11 m, coral mud, 9 Sep. 1874, C379253 (1v). **Papua New Guinea.** Lolorua Is., SW Port Moresby, 9°30'S 147°6.5'E, 13–18 m, 21 June 1970, C379256 (7v), and 9°30'S 147°7'E, 13–22 m, 21 June 1970, C379257 (21v).

Description

Shell. Maximum length 1.58 mm, maximum height 1.53 mm, inequilateral, with umbo slightly displaced from middle, prosogyrate and white or bone coloured. Inflation ratio, 1.07–1.74.

Prodissoconch. Maximum length 180 µm, consisting of prodissoconch I. Prodissoconch I with five indented areas in radial pattern and thickened rim.

Dissoconch. Lunule and escutcheon long and broad with commarginal sculpture. Outline triangular or rectangular with convexly angled anterior and posterior slopes, sharply angled anterior and posterior ends. External sculpture of about 59–61 fine commarginal ribs, creating a fenestrate pattern between radial ribs, with scabrous structures on the 9–10 strong radial ribs. Inner margin with 9–10 denticles. Hinge plate wide. Lateral

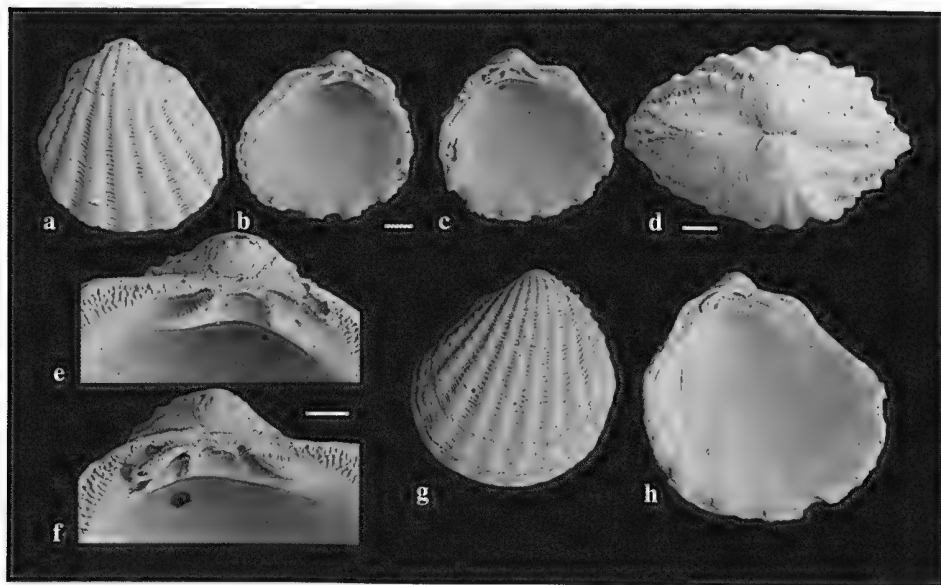


Fig. 30. *Isodontocardia microcardia*. a–f, Paratypes, C379259 Amazon Bay, Papua New Guinea. g, h, Murray Island, Torres Strait, Queensland. g, Holotype C388188. Scale bars: a–c, g, h, 200 µm; d, 100 µm; e, f, 100 µm.

teeth area dorsally extended into plate-like structure, with sculptured/wrinkled surface. Lateral teeth positioned just ventrally from these surface ripples. Two lateral teeth in each valve. Teeth all longer than half length of dorsal slopes and consist of anterior lateral (LAI) and posterior lateral (LPII) in right valve and anterior lateral (LAI) and posterior lateral (LPII) in left valve. Right valve anterior cardinal tooth (CA3) oblique and strong. Posterior cardinal tooth (CP3) present, divided into cardinal elements CP3a,b. Left valve anterior cardinal tooth CA4 arched, divided into cardinal elements CA4a,b. Posterior cardinal teeth (CP2 and CP4) dorsally connected. Internal ligament 60 μ m long, rounded, in resilium.

Dimensions. See Table 19.

Table 19. Measurements of specimens of *Isodontocardia microcardia* n. sp.

	SL (mm)	SH (mm)	PL (mm)	SI (mm)	SL/SI \times 2
<i>Isodontocardia microcardia</i> , holotype, C388188 (Fig. 30g)	1.52	1.57	0.17	0.71	1.07
<i>Isodontocardia microcardia</i> , paratypes, C379259	1.49	1.48	0.13	0.51	1.46
	1.48	1.40	0.16	0.54	1.37
	1.58	1.53	0.17	0.60	1.32
	1.51	1.50	0.14	0.57	1.32
	0.94	0.90	0.18	0.27	1.74

Distribution

Northern Territory, Queensland and Papua New Guinea (Coral Sea), subtidal to continental shelf, 0–65 m depth. Found in mud or sand. This species is only known from shells.

Etymology

Micro from Greek for 'small' and *cardia* from Greek for 'heart'.

Excluded taxa

Family ?NEOLEPTONIDAE

Puyseguria chapmani (Gatliff & Gabriel, 1912a)

Condylocardia chapmani Gatliff, & Gabriel, 1912a: 167 (type locality: off Portsea, Port Phillip, Victoria, dredged. Holotype NMV F481). – Macpherson & Chapple, 1951: 149; Kershaw, 1955: 296; Lamprell & Healy, 1998: 168, fig. 478.

Benthocardiella chapmani (Gatliff & Gabriel, 1912a). Macpherson & Gabriel, 1962: 321.

Remarks

Puyseguria chapmani was initially described as a species of *Condylocardia*. The hinge teeth, flat prodissoconch and shape suggest placement in *Puyseguria* Powell, 1927, although compared to the type of *Puyseguria* (*P. cuneata* Powell, 1927) the hinge teeth are transposed.

This species emphasises, like the two *Benthocardiella* species described above, a possible close relationship between the Condylodiinae and Neoleptonidae.

Family GALEOMMATIDAE *sensu* Ponder (1998)

Mysella ovata (Hedley, 1906a)

Condylocardia ovata Hedley, 1906a: 539, pl. 31, figs 5, 6 (type locality: Manly Beach, Sydney, New South Wales. 33°48'S, 151°17'E, pres. L. Parkes. Holotype C024500). – Hedley, 1906b: 465; Verco, 1907: 109; Verco, 1908b: 18; Gatliff & Gabriel, 1908: 389; Verco, 1908a: 359; Hedley, 1918: M17.

Calvitium glabra Laseron, 1953: 46, figs 32 and 32a,b (type locality: Gunnamatta Bay, Port Hacking, Sydney. Syntypes C090588 (48 v)). – Lamprell & Healy, 1998: 166, fig. 464.
Condyllocuna ovata (Hedley, 1906b). Laseron, 1953: 40, figs 17, 17a. – Cotton, 1961: 206, fig. 210; Macpherson & Gabriel, 1962: 321; Jansen, 1995: 101, fig. 425; Lamprell & Healy, 1998: 170, fig. 482.

Remarks

This taxon resembles species of *Condyllocuna* superficially although it differs markedly in hinge detail. The cardinal CA3 is larger, longer and more or less detached from the anterior margin. The posterior cardinal in the right valve is bigger than in *Condyllocuna*. There are no real cardinals in the left valve. The shell and hinge agree with species of *Mysella* Angas, 1877.

Examination of the type specimens of *C. ovata* and *C. glabra* using SEM shows that these two taxa are synonymous. Since *C. glabra* is the type species of *Calvitium* Laseron, 1953 (Neoleptonidae), *Calvitium* becomes a synonym of *Mysella*.

Discussion

The aim of this review was to produce a revision of the Condyllocardiinae based on available characters. Unfortunately only the shells of all but one species of Condyllocardiinae (*s.s.*) are known to date. Since the review is based on shells alone, future analyses of anatomical and molecular characters are required to underpin the taxonomic decisions made.

As a consequence of the lack of available live material, virtually nothing is known about where the species live or what their role might be in marine ecosystems. With the descriptions provided herein it is hoped that more work on the group will be stimulated.

The biggest challenge in this revision was to correctly identify the hinge teeth. Although labelling of the lateral teeth follows Bernard's (1898) scheme, several deductions had to be made in respect to the cardinal teeth. The absence of ontogenetic sequences from prodissoconch through juvenile to adult in most species made direct observations of cardinal teeth ontogeny impossible. The deductions made are largely based on adult hinge teeth similarities (Fig. 31). The lines in Fig. 31 that link the cardinal teeth elements do not represent any evolutionary sequence but simply connect teeth that are considered homologous. The anterior cardinal teeth of the right valve consist of a dorsally recurved and subdivided cardinal CA3 in *Benthocardiella* and *Condyllocardia* following Bernard's (1898) scheme. In all other genera treated herein, this tooth is not subdivided. However, in *Austrocardiella* a small fold proximal to the ligament is apparent and has here been labelled CA5. The posterior cardinal teeth in the right valve are mostly consistent throughout the subfamily with the exception of *Condyllocuna tricosia*, in which these elements are undeveloped or reduced, and *Benthocardiella*, in which CP2 is absent.

The most striking difference in the cardinal teeth elements of the left valve is the presence of CA2 in *Benthocardiella* and *Condyllocardia* and the absence of a CP2 in *Benthocardiella*.

The species *C. subradiata* and *C. notoaustralis* are variable and appear to show clinal integration in New South Wales. Both require further study to clarify their status. *Condyllocardia limaeformis*, *C. notoaustralis*, *Condyllocuna projecta* and *C. tricosia* have closely similar relatives outside Australia in New Zealand, on St Paul Island, and in South Africa. The development of these widespread species-complexes is certainly non-pelagic and likely means of dispersion would be by rafting, utilizing macro-algae haptors, thalli or other rafting objects. Comparative studies on Australian, New Zealand, South Africa and St Paul Island taxa would be useful in determining character differences between the taxa.

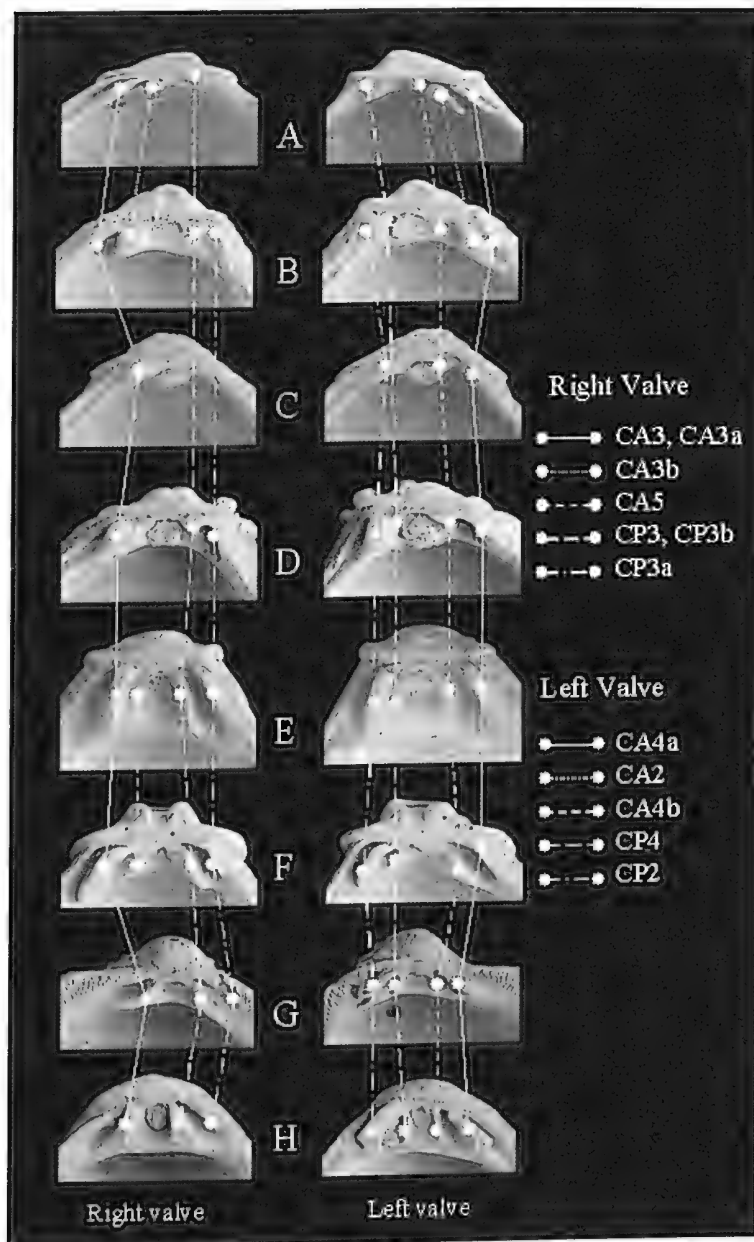


Fig. 31. Homologous hinge teeth elements linked between representatives of condyllocardiine genera. A, *Benthocardiella burtonae*. B, *Condyllocardia limaeformis*. C, *Condyllocardia tricosia*. D, *C. projecta*. E, *Austrocardiella trifoliata*. F, *A. pouli*. G, *Isodontocardia microcardia*. H, *Cunanax pisum*. The link between CA3b in A and B indicates the secondary subdivision of CA3 only believed to be present in *Benthocardiella* and *Condyllocardia*. See Fig. 1 for explanation of symbols.

Previously used terms for the mode of reproduction in the condylocardiines are confusing. The term 'larvae' was used for the prodissoconch stage in the female suprabranchial cavity by Salas and Rolán (1990), but as the presence of velum or other larval characters have not been proven, this term should not be applied (see Levin and Bridges 1995). The presence of two distinct morphological areas on the prodissoconch was interpreted as prodissoconch I and II (prodossoconch I being the centre of the prodossoconch) by Salas and von Cosel (1991) against the traditional usage of these terms in connection with pelagic developing larvae of either the lecithotrophic or planktotrophic type (Jørgensen 1946; Ockelmann 1965). However, the presence of these prodossoconch parts is independent of the ontogenetic pathway because some embryos develop two shell parts, even if they are brooded and lack any pelagic development.

The inner shell area, here referred to as prodossoconch I, is created by the shell gland of the embryo (see Ockelman 1965), viz., not the mantle edge, following the interpretation of Salas and von Cosel (1991) in other condylocardiines. *Condylocuna jimbecki* (Fig. 20s) provides evidence for this theory, as the first shell (prodossoconch I) possesses characters indicative of ontogenesis by a complex shell gland. Firstly, the microstructures consist of pits with no commarginal pattern, and secondly the complex calcified structures that create the appearance of three radiating indentations could not have been created by the mantle edge.

The second area has fine commarginal lines and a radial pattern created by the mantle edge of the embryo. It is this part that is prodossoconch II as defined by Ockelmann (1965). This resolution follows Salas and von Cosel's (1991) terminology.

The available information indicates that the reproductive mode in the condylocardiines is brooding and lecithotrophic, i.e. brooded embryos that live on yolk supplied in the egg. The likely embryonic morphogenetic pathway is direct development (i.e. a larval stage is lacking) but this needs to be confirmed.

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Destruction of *Indoplanorbis exustus* (Planorbidae) eggs by *Pomacea bridgesi* (Ampullariidae)

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Abstract.

Six size classes (5–9 mm, 10–14 mm, 15–19 mm, 20–24 mm, 25–30 mm and 30–34 mm) of the ampullariid snail *Pomacea bridgesi* were experimentally exposed to 10–25 egg capsules of the planorbid snail *Indoplanorbis exustus*. With one exception, in all the trials performed with the snails of the four highest size classes, egg capsules of *I. exustus* were destroyed by *P. bridgesi*, whereas in the 5–9 mm and 10–14 mm size classes, egg capsules were destroyed in 20% and 68.96% of trials respectively. An individual of *Pomacea* belonging to each of the six size classes could destroy, on average, 0.28, 2.27, 2.38, 3.82, 3.75 and 3.62 egg capsules, respectively, during a period of 24 hours. Irrespective of size class, an individual could consume 0–6 (average 1.57 ± 0.08 s.e.) and damage 0–9 (average 1.14 ± 0.10 s.e.) egg capsules per 24 hours. On average there are about 20 eggs in each capsule, so an individual of *P. bridgesi* would be able to destroy around 60 eggs of *I. exustus* daily. These observations are relevant to possible biological control of *Indoplanorbis*.

Introduction

The planorbid snails of the species *Indoplanorbis exustus* (Deshayes, 1834) are involved with the spread of schistosomiasis, fasciolosis and amphistomiasis in domestic animals (Malek and Cheng 1974; Chen *et al.* 1986; Biswas 1991) and sometimes fasciolosis and amphistomiasis in humans (Biswas 1991) in a number of South-East Asian countries (Subba Rao 1989). Various attempts to control these snails have failed, and searches for suitable biological control agents are still in progress. In 1992, the ampullariid snail *Pomacea bridgesi* (Reeve, 1856) was introduced in West Bengal, India, from Thailand in connection with the aquarium trade (Raut and Aditya 1999). They are thriving well in different rearing centres of West Bengal, fulfilling Baker's (1998) prediction regarding establishment of *Pomacea* snails in India. We had the opportunity to develop a stock in our laboratory by culturing a few individuals received from a trader (Raut and Aditya 1999). In our laboratory, the snails fed on a number of food items including the egg masses of the fresh water vector snails *I. exustus* (Aditya and Raut 2001), which prompted us to carry out experiments to ascertain the efficacy of *P. bridgesi* in the control potential of *I. exustus*. The results are presented here.

Materials and methods

Ten glass aquaria, each measuring 14 cm³ were used for the experiments. Each aquarium was filled with pond water (2.5 L). Forty to fifty reproducing individuals of *I. exustus* were placed in each aquarium and fed with lettuce. After 24 hours the aquaria were emptied of water and snails. The number of egg capsules deposited on the glass wall of the aquaria was counted and recorded. If fewer than 10 egg capsules were recorded, the aquarium was not used for experiment. An individual of *P. bridgesi* was taken from the laboratory culture stock and allocated to one of the following size classes (shell length): 5–9 mm; 10–14 mm; 15–19 mm; 20–24 mm; 25–29 mm; and 30–34 mm. Fresh pond water and the *Pomacea* were added and left for 24 hours. After 24 hours the numbers of egg capsules consumed and damaged (due to rupturing and biting) were counted. Each individual of *P. bridgesi* was used only once in the experimental trials. A total of 169 trials (see Table 1) were performed. In each case, there were 10–25 egg capsules of *I. exustus*

in each aquarium and in all the experiments the snails were not offered any other kind of food. In some cases, bitten and ruptured egg capsules were kept under observation to note the fate of the eggs. One-way analysis of variance (ANOVA) was applied (Campbell 1989) to determine the effects of the size classes on the rate of destruction of *I. exustus* egg capsules. All data are presented as average \pm standard error (s.e.).

Results

Destruction of *Indoplanorbis exustus* eggs varied with the experimental trials and the size of the individuals of *Pomacea bridgesi* used (Table 1). Of the 25 trials with 5–9 mm *P. bridgesi*, egg capsules were damaged in only five (20%) trials (two with 8 mm and three with 9 mm individuals) with 1–2 egg capsules damaged through repeated biting. Out of 29 trials with 10–14 mm *P. bridgesi*, nine snails did not touch the egg capsules at all and 11 snails ruptured 2–6 egg capsules. On average, each individual swallowed 2–4 and ruptured 1–2 egg capsules in each trial with 14 mm *P. bridgesi*. All the 32 (100%) trials carried out with 15–19 mm snails were effective in destroying the egg capsules, though the rate of damage due to consumption was higher (63.16%) than that due to rupturing (36.84%). *Pomacea bridgesi* in the 20–24 mm size class consumed almost three times more egg capsules than the number of egg capsules they ruptured, i.e. 73.8% were consumed and 26.2% were damaged. Of the 32 trials with 25–29 mm snails, egg capsules were destroyed in 31 (96.87%) cases. All the 29 (100%) 30–34 mm snails destroyed between 1 and 7 (average 3.62 ± 0.23) egg capsules. Individuals belonging to the 25–29 mm and 30–34 mm size classes consumed and ruptured (on average) 63.33% and 36.67% and 53.33% and 46.67% egg capsules respectively.

Irrespective of size class, out of a total 169 trials performed, 139 (82.25%) *Pomacea* were effective in destroying the egg capsules of *I. exustus*. Of the total 458 egg capsules destroyed, 266 (58.08%) were swallowed and 192 (41.92%) were ruptured by the predators. Each individual of *P. bridgesi* destroyed, on average, 2.71 ± 0.11 egg capsules (1.57 ± 0.08 due to feeding and 1.14 ± 0.10 due to rupturing) during a period of 24 hours. In all cases

Table 1. Number (range and mean \pm s.e.) of *I. exustus* egg capsules consumed, damaged and destroyed by *P. bridgesi* individuals from different size classes during a 24 hour period

Size classes of <i>P. bridgesi</i>	Number of trials (1 individual per trial)	Number of <i>I. exustus</i> egg capsules		
		Consumed	Damaged	Destroyed (consumed + damaged)
5–9 mm	25	0	0–2 (0.28 \pm 0.11)	0–2 (0.28 \pm 0.11 ^{abcd})
10–14 mm	29	0–4 (0.83 \pm 0.21)	0–6 (1.45 \pm 0.21)	0–6 (2.27 \pm 0.23 ^{ac})
15–19 mm	32	0–5 (1.5 \pm 0.21)	0–3 (0.88 \pm 0.18)	1–5 (2.38 \pm 0.2 ^{efgh})
20–24 mm	22	1–6 (2.82 \pm 0.36)	1–4 (1.00 \pm 0.21)	3–6 (3.82 \pm 0.19 ^{bf})
25–29 mm	32	0–6 (2.38 \pm 0.26)	0–9 (1.38 \pm 0.35)	0–9 (3.75 \pm 0.38 ^{cg})
30–34 mm	29	0–5 (1.93 \pm 0.2)	0–7 (1.69 \pm 0.26)	1–7 (3.67 \pm 0.22 ^{dh})
Overall	169	0–6 (1.57 \pm 0.08)	0–9 (1.14 \pm 0.1)	0–9 (2.71 \pm 0.11)

Groups sharing a common letter differ significantly, for f: $P < 0.05$, in all other cases $P < 0.001$.

the eggs belonging to the bitten and ruptured capsules perished. A summary of the results is given in Table 1. ANOVA tests clearly show that larger sized *P. bridgesi* cause significantly ($P < 0.001$) greater destruction of *I. exustus* egg capsules.

Discussion

The results suggest that *Pomacea bridgesi* could help to reduce the abundance of *Indoplanorbis exustus* through egg predation. *Indoplanorbis exustus* deposits 2–43 (average 20) eggs per capsule (Islam 1977; Raut and Ghosh 1985; Raut 1986; Raut *et al.* 1992). The results indicate that large individuals of *P. bridgesi* are capable of destroying around three egg capsules in 24 hours, thus destroying at least 60 embryonic-stage individuals of *I. exustus* daily. Furguson (1978), Pointier *et al.* (1988) and Cazzaniga (1990) have also reported ampullariid predation of the eggs, young and adults of *Biomphalaria* and have suggested several species of Ampullariidae as agents for the control of planorbid snails. Because *P. bridgesi* individuals in the 20–24 mm size class are effective in destroying eggs of *I. exustus*, and there exists no significant difference in the rate of predation among the members of even larger size classes, large *P. bridgesi* (>20 mm in length) can be considered as potentially suitable for a biological control program. *Indoplanorbis exustus* produces about 60 egg capsules in its average life span of four months (Raut *et al.* 1992). Under conditions similar to those in the experiments described in this paper, it is likely that a single *P. bridgesi* in one of the most effective size classes could destroy all these egg capsules within three weeks.

Pomacea bridgesi could be considered as a potential biological agent for the control of *I. exustus* in India and other countries. However, careful studies are required to ascertain whether this species would cause unacceptable environmental impacts. In many countries where they have been introduced, *Pomacea* snails, especially *P. canaliculata* (Lamarck), have contributed to the decline of native species (e.g. *Pila* in South-East Asia) (Acosta and Pullin 1991), the damage of paddy plants, especially rice (Godan 1983) and taro (Cowie 1993), and are suspected of acting as intermediate hosts of certain human diseases (Cheng and Alicata 1965; Hanning and Leedom 1978). Extreme caution should therefore be taken before employing these snails in any form of biological control. Since *Pomacea* has the potential to colonise Bangladesh, Burma and rice-producing areas of Australia (Baker 1998), the present information may prove helpful in assessing the impact of these predaceous snails, if ever introduced, on the ecology of the habitats concerned.

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BOOK REVIEW

Tropical Deep-Sea Benthos. Volume 22.

Edited by Philippe Bouchet and Bruce Marshall.

Published 2001, by the Muséum National d'Histoire Naturelle, Paris. (Also Volume 185 of the Mémoires du Muséum National d'Histoire Naturelle.) 406 pages. Hardback. Euro 67.08, approximately AU\$115.

Scientists from the Muséum National d'Histoire Naturelle, Paris and the Institut de Recherche pour le Développement (IRD, formerly ORSTOM) have been conducting extensive collecting expeditions in the Indo-West Pacific Ocean since 1985. The field program has been led by Dr Bertrand Richer de Forges using the Noumea based Research Vessel *Alis*. Dredging and trawling have been centred on New Caledonia but also include work in the Philippines, Vanuatu, Tonga, the Marquesas, Norfolk and Loyalty Ridges and other areas. In fact, the paper by Bruce Marshall on *Acesta* records *A. saginata* Marshall, 2001 from 23°S on the Norfolk Ridge to 56°S on the Macquarie Ridge. The studies have been conducted in depths ranging from shallow lagoons in coral reef atolls to below 2000 metres. An incredibly wide variety of organisms has been collected and sorted. The Muséum team has gone to considerable effort to make the material available to the leading world experts on particular groups. Many scientists have had the opportunity of working on the material in Paris and extensive amounts of material have been loaned to other institutions. The results have been published in 21 volumes of *Résultats des Campagnes MUSORSTOM*. Three of these volumes (one in 1981, two in 1986, and 16 in 1997) are devoted entirely to molluscs and others include mollusc sections.

Tropical Deep-Sea Benthos Volume 22 is the continuation of the MUSORSTOM series. The new title is intended more accurately to describe the series and to highlight the fact that the volumes are published primarily in English: ten papers in the present volume are in English and two are in French. The 16 authors of Volume 22 are, in general, well-known experts in their respective groups and come from eight different countries.

Volume 22 deals entirely with molluscs and includes papers on Aplacophora (five new species described), Polyplacophora (five), Pectinoidea (two), *Acesta* (one), Spondylidae (eight), Poromyoidea (five), Triviidae (nine), Muricidae (one genus, eleven species), Conoidea (17), Pleurobranchiidae (one), Phyllidiidae (12) and Cephalopoda (one). Thus, the richness of the fauna collected continues to be validated, with one new genus and 77 species described. Many of the new taxa are quite interesting. Five of the six aplacophorans found in the western Indian Ocean and Arabian Sea by Dmitry Ivanov and Amélie Scheltema are new species; none of the six has been reported in the Atlantic or Pacific Oceans. The newly described *Sepia subplana* Lu and Boucher-Rodoni, 2001 from banc Bayonnaise is the eastern-most record of a cuttlefish in the Pacific Ocean.

However, the volume is much more than a simple compendium of new species. The considerable material available means that there is a wealth of information generated about previously known species – a total of 182 species are discussed in the volume. For example, the paper on Spondylidae by Kevin Lamprell and John Healy describes eight new species but this only represents a quarter of the 32 species discussed. The family Phyllidiidae was recently revised in a major work by David Brunckhorst (*Records of the Australian Museum, Supplement* 16; 1993). New material made available through the MUSORSTOM collecting allowed Ángel Valdés to examine a total of 15 species, 12 of which were new. In contrast

to the shallows where *Phyllidia* is dominant, over 70% of the species at depths of 100–500 metres, and both of the species found deeper, are *Phyllidiopsis*.

In addition to the high quality of science presented in the MUSORSTOM series, *Tropical Deep-Sea Benthos* continues the earlier high quality standards of editing and presentation. The volume is a substantial credit to the two well-known malacologists who edited it, Philippe Bouchet of the Muséum National d'Histoire Naturelle, Paris and Bruce Marshall of the National Museum of New Zealand. The volume is well laid out and illustrations are good. There are even a number of colour plates showing some of the more spectacular species. The volume is hard bound, which means that it will remain durable even after repeated consultation. The cover is attractive, with a green background. The top of the front cover is a photograph of a deep-water habitat. Along the left side there are several colour photographs of the vessel used and the animals collected. A colourful *Spondylus* is on the lower right.

This volume is a welcome addition to the MUSORSTOM series and will be of considerable interest to scientists and amateurs interested in molluscs around the world. Additional information can be found at the MNHN websites: www.mnhn.fr/publication/memoire/mem.html (for the series) and www.mnhn.fr/publication/memoire/m185.html (for this volume).

Fred Wells
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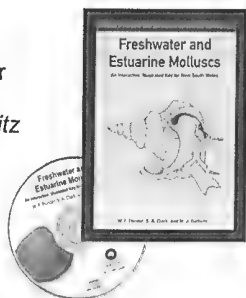


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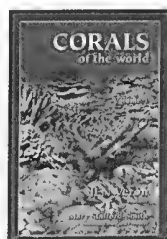


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